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THE JOURNAL OF ANIMAL ECOLOGY

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CONTENTS

PAGE

J. S. Hough. The effect of wind on the distribution of Cynipid galls caused by *Neuroterus lenticularis* Olivier 165

W. B. Yapp. The population of rooks (*Corvus frugilegus*) in west Gloucestershire. II 169

David and Elizabeth Lack. Further changes in bird-life caused by afforestation 173

C. B. Williams. Seasonal changes in flight direction of migrant butterflies in the British Isles 180

Anne D. Brian. The pollen collected by bumble-bees 191

J. A. R. Miles and J. B. Shrivastav. Ornithosis in certain sea-birds . 195

E. D. Le Cren. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*) . 201

C. R. Ribbands. The flight range of the honey-bee 220

H. Barnes, D. J. Crisp and H. T. Powell. Observations on the orientation of some species of barnacles 227

T. B. Bagenal. A note on the papers of Elton and Williams on the generic relations of species in small ecological communities . 242

C. B. Williams. Intra-generic competition as illustrated by Moreau's records of East African bird communities 246

Reviews 254

Books received 258

Notices of publications on the Animal Ecology of the British Isles . 259

Notice to contributors 269

THE EFFECT OF WIND ON THE DISTRIBUTION OF CYNIPID GALLS CAUSED BY *NEUROTERUS LENTICULARIS* OLIVIER

BY J. S. HOUGH

*Department of Botany, University of Sheffield**

(With 4 Figures in the Text)

During investigations on the morphogenesis of the gall induced in oak leaves by the Cynipid larva *Neuroterus lenticularis* Olivier, my attention was drawn to the uneven distribution of these spangle galls. This communication reports the results of this examination and attempts to correlate the occurrence of galls with the dispersal of gall wasps by wind currents.

The work was carried out between June and September 1950 on areas 2–3 miles west of the centre of the city of Sheffield.

Felt (1940) considered that although the Cynipidae are not strong fliers, this does not make impossible wide distribution by air currents. During the summer of 1927, he collected six different species of gallwasps from the gutters of the roof of the State Education Building at Albany, New York. The gutters were 125 ft. above the sidewalk. Five out of the six species collected were well-recognized oak species, although there were probably no oaks within a mile of the building. Felt therefore concluded that the insects must have drifted in the wind because of their limited capacity for flight. He also considered convectional currents to be important. The probability of extended, though presumably exceptional, wind-drift of these insects, he concludes, is suggested by the practically world-wide distribution, subject to the local occurrence of suitable hosts, of a number of tropical or subtropical species.

Freeman (1945) sampled the aerial population of insects above an area of agricultural land in Lincolnshire at heights of 10, 177 and 277 ft. over a front of 4400 ft., by nets flown from the masts of a beam-wireless station. He found that while most of the Hymenoptera tended to occur during the warmer months, the Cynipidae persisted throughout the period of sampling (March to November inclusive).

Although Dr Freeman gives no more details of the capture of Cynipidae in his paper, he has written to the present writer giving further information. From this it is clear that the nets near the ground captured more insects than the nets at higher levels. The total numbers of Cynipidae caught at 10, 177 and 277 ft. were 98, 9 and 5 respectively. Dr Freeman found that the maximal densities of the Cynipidae occurred in June and September.

During the course of the present investigation, numerous Cynipidae have been found in localities far from any suitable host plant. These captures suggest that Cynipidae are carried considerable distances by wind-drift. It must be pointed out, however, that not all Cynipidae are associated with plant galls. A few are parasitic on dipterous flies, and closely resemble the gall-forming species so that erroneous identification is easy. Mr Hincks, the assistant curator of entomology at Manchester Museum has, however, observed swarms of Cynipidae being carried by the wind, and he identified these insects as gall-forming species.

Indirect evidence is obtainable by finding the maximum heights at which spangle galls occur. By the use of binoculars, the galls were seen on leaves between 30 and 40 ft. up oak trees. Red-currant galls may be found at least 20 ft. from the ground and possibly at greater heights. If it be possible for insects to rise to these heights from ground-level in order to oviposit, it appears probable that they can travel far greater horizontal distances. It is true that in some instances the insects may hatch, mate and oviposit without descending to the ground. But where the gall falls to the ground to finish its development, as in the case of the spangle gall, this objection does not arise.

The following observations can be explained if it be assumed that migration can occur. On 6 June 1950, at Bingham Park, there were thousands of *N. baccarum* wasps ovipositing upon the leaves of the oak bushes. At this time, however, fewer than ten currant galls had hatched in the area. The wasps all arrived between 4 p.m. on 5 June and 10 a.m. 6 June. Their numbers were so great that it was impossible to give an accurate estimate, but in the area specially selected for study, it was calculated that between 1000 and 1500 wasps were present. Examination of other areas in the park showed that the wasps were present in large numbers, but their density was not as great. On 7 June, there were still many insects but the numbers soon decreased quickly until none were to be found on 9 June.

* Now at The College, Keele, near Stoke-on-Trent.

The number of galled buds in the specially selected area was very near 200. Of these, 100 were examined and the calculated average number of currant galls per galled bud was found to be 3·9; 200 galled buds would therefore bear about 780 galls. On 8 June, however, a random sample of 100 currant galls was examined and 21% only were found to have hatched. The rest were parasitized.

The 780 galls would therefore produce about $780 \times \frac{1}{2} \times 21/100$ ovipositing females, or approximately 82. Galls collected and hatched in the laboratories had yielded approximately equal numbers of males and females: the calculation has been made assuming this to be true in the case under review.

Now 82 female wasps were a tiny fraction of the total numbers of wasps which oviposited in the special area. It is known, moreover, that the galls in the area produced their insects later than 6 June, the day when so many were seen. From what sources could these gallwasps have come?

the hot sunny weather was such as to set up strong thermal currents. This was confirmed by reports from a local gliding club which was able to use the thermals to advantage.

In September the whole of Bingham Park and adjacent woodland was examined carefully to see if there were any indications that the gallwasps had been carried there by wind-drift. The density of galling in Bingham Park and an adjacent area to the west, Trippet Wood, is shown in Figs. 1 and 2. Especially where the trees were large and close together, as in Trippet Wood, the northern branches were the most heavily galled and the extent of galling decreased towards the southern edges of the woods. Where trees were widely spaced, this pattern of distribution was not evident, although possibly a few more galls were to be found on the northern branches. Those parts of Bingham Park with an intermediate tree-spacing were also intermediate in the extent to which galling was localized, the northern branches being heavily galled at the northern edge of the wood

Table 1. *Meteorological data from Graves Museum, Weston Park, Sheffield*

	Wind direction and force (Beaufort scale)		Screen temperature (° F.)		
Date	9 a.m.	9 p.m.	Max.	Min.	Sunshine (hr.)
Sunday, 4 June	SE. (3)	S. (1)	80·4	55·3	13·5
Monday, 5 June	NNE. (1)	NE. (1)	81·3	57·2	12·8
Tuesday, 6 June	NE. (1)	S. (1)	86·2	57·7	12·7
Wednesday, 7 June	SW. (2)	WSW. (1)	87·1	61·7	14·9
Thursday, 8 June	WSW. (2)	W. (3)	65·3	56·2	2·1

The insects might have come from bushes in the park outside the special area. This seems unlikely, because there were fewer galls per bush outside that area whilst the percentage which hatched was about the same. These bushes had also large numbers of ovipositing *N. baccarum* wasps upon them between 5 and 8 June.

A further possible source was from galls high up in the mature oaks of the park. Many of these trees were scaled with a ladder but only two of them were found to be galled. Thirty galls of *N. baccarum* were found 20 ft. up one tree whilst three galls were found at 15 ft. on another. Twenty-six of these galls were parasitized so that the number of female wasps from this source was small.

It was decided to investigate the possibility of the wasps having been brought over some distance by wind-drift. The meteorological department at the Graves Museum, Weston Park, kindly supplied the data for the period. These are set out in Table 1. Between 9.0 a.m. on 5 June and 9.0 a.m. on the 6th the wind direction was predominantly north-easterly, though its velocity was little more than 3 m.p.h. The barometer was high throughout, no rain fell, and

but this pattern of distribution being less evident towards the south. The diagrams show that, in the case of Trippet Wood, the houses have apparently screened the lower edge from infection. In Bingham Park, however, where the houses are below the level of the edge of the wood and more distant from it, the trees at this northern edge have been heavily galled.

The distribution suggests strongly that gallwasps were carried into the areas by wind-drift from the north or north-east, though it has been impossible to locate their source with certainty. Currant galls were not found in the woodland just north of the Park, but this does not rule out the possibility of there having been a few. Fig. 1 shows the obstacles between this woodland and the Park.

A north-south section of the country to the north of Bingham Park is shown in Fig. 3. This section shows that there are two large areas of woodland to the north of the site. These are the Rivelin Valley oakwoods and the Beeley Park oakwoods. These were examined in September to see if the distribution of galls in the woods would shed further light on the problem.

The density of spangle-gall infection in the Rivelin Valley oakwoods was high. On the upper slopes there were many narrow treeless gullies (about 10 yd. wide and 6 ft. deep) running in a north-south direction (Fig. 4). The trees at the edges of these gullies were very heavily galled, especially those on the west side of the gullies. At the high southern limit of the woods the trees were more heavily galled on their north-easterly side except for those effectively shielded from the north by other large oaks. The latter were always heavily galled. Exposed solitary oak bushes above the general southern edge of the oakwoods were heavily galled, especially the branches on the northern side. This strongly suggests that the gallwasps were swept from the Rivelin Valley oakwoods by a north or north-easterly wind.

Beeley Park had a higher density of the spangle galls near the river, with few on the upper northern slopes. The total density of galling was much lower than for the Bingham Park and Rivelin Valley oakwoods. It was, however, impossible to find any strong evidence that transport of the insects by wind, to or from the area, had occurred.

The fact that these oakwoods are situated on a south-facing slope may account in some way for their difference from the Bingham Park and Rivelin Valley oakwoods.

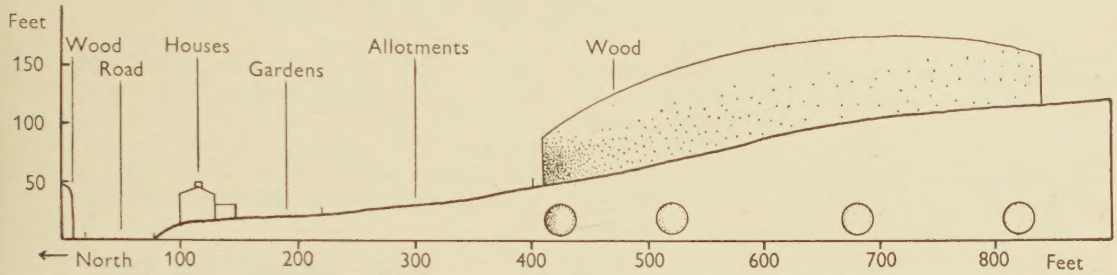

Fig. 1. A diagram of a north-south section of Bingham Park. Stippling indicates the relative density of gall occurrence. Circles (not to scale) represent trees in plan view.

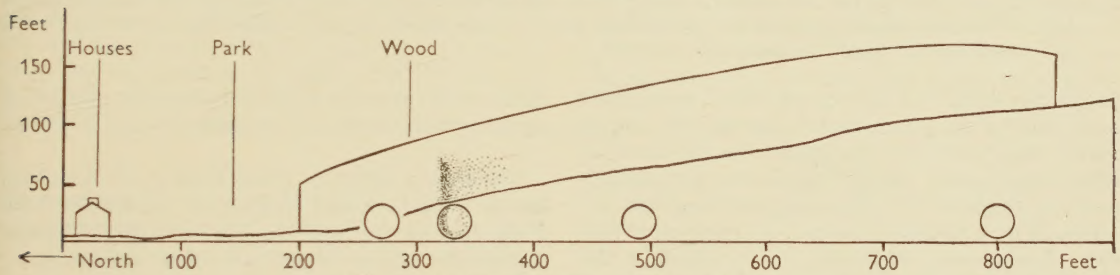

Fig. 2. A similar diagram of Trippet Wood.

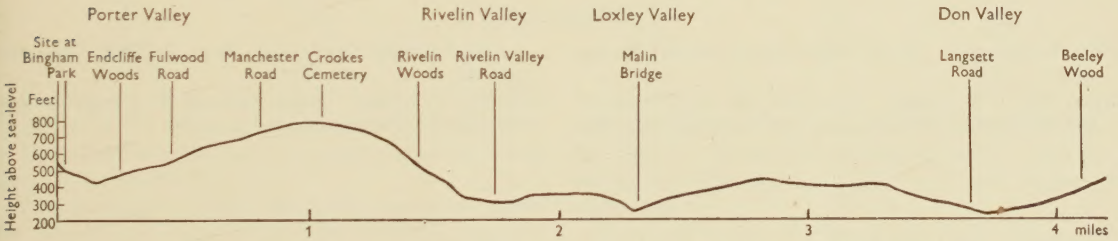

Fig. 3. A diagram of a north-south section of the country to the north of Bingham Park.

It is the writer's view, although the densities of spangle galls (and also currant galls in the case of Bingham Park and Rivelin Valley oakwoods) in the various districts of Sheffield are the only grounds for it, that the gallwasps were carried by wind-drift from the Rivelin Valley oakwoods by a north-easterly wind. He is also of the opinion that migration due to wind-drift is an important factor in the distribution and occurrence of Cynipid galls.

Referring to the genus *Diplolepis* (*Dryophanta*) Niblett (1940, p. 145) has stated 'There is one

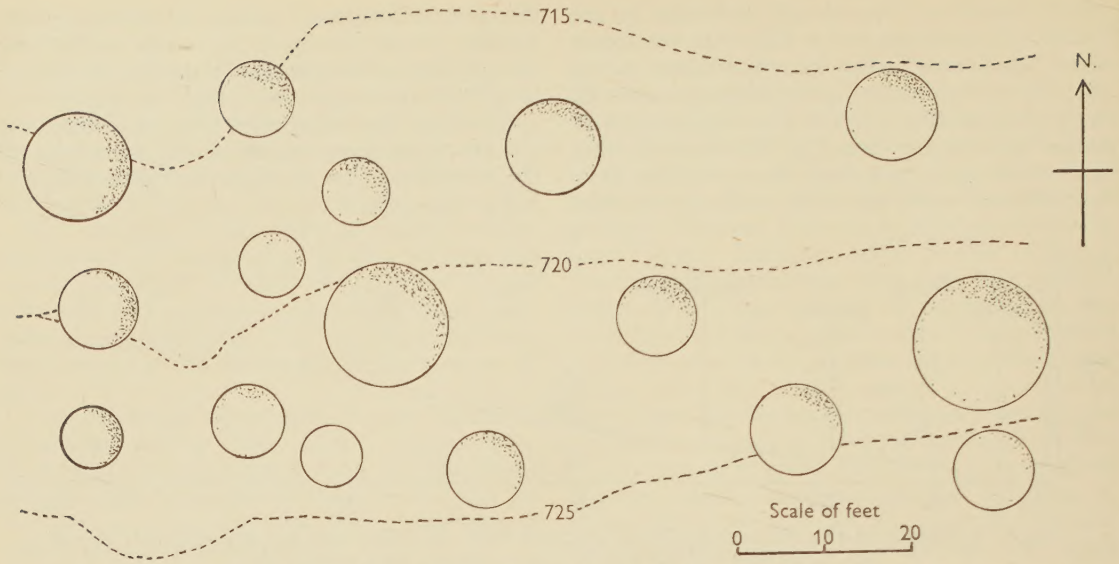

Fig. 4. A diagram showing gall occurrence at the southern ridge of the Rivelin Valley oakwoods. The trees are shown in plan view and stippling represents the relative density of the galls. A gully is shown on the left by means of contour lines of height in feet above sea-level.

peculiarity which has been noted before, and applies to all galls of the genus, that is the entire or almost entire disappearance of the galls from the localities where they could usually be found, for varying periods, followed by their reappearance and recurrence for a number of years'. It is suggested that this phenomenon, which is very evident in the Sheffield district for all types of Cynipid galls, is due in some measure to the insects being carried by wind-drift, an obviously hazardous mode of dispersal.

The author wishes to thank Prof. A. R. Clapham for his helpful criticism and advice, and the Sheffield Parks Department and the Meteorological Department of the Graves Museum for their assistance.

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THE POPULATION OF ROOKS (*CORVUS FRUGILEGUS*) IN WEST GLOUCESTERSHIRE. II.

By W. B. YAPP

Department of Zoology, University of Birmingham

The area surveyed, and the results for 1933, are described in a former paper (Yapp, 1934). Nests were counted by the same methods in each of the 7 years, 1933–9, and again in 1944. The totals are shown in Table 1, col. 2; detailed information has been deposited at the Edward Grey Institute at Oxford.

THE NUMBER OF NESTS

The general picture is of a steady rise, broken by fairly sharp falls in 1936 and 1938. The series is rather short for statistical treatment, but for what it is worth the mean of the continuous run of 7 years is 1053, and the standard deviation is 60. Whereas the 1936 fall is therefore probably not significant, that of 1938 may be. An attempt has been made to relate this fall to other factors.

Table 1. *Numbers and densities of rooks' nests*

Year	Total nests	Nests/sq.mile	Rooks/acre cereals	Rooks/acre cereals, roots and potatoes	Rooks/acre arable
1933	1009	15·4	1·40	1·05	0·42
1934	1059	16·1	1·72	1·25	1·05
1935	1075	16·4	1·54	1·19	1·04
1936	1052	16·0	1·64	1·28	1·08
1937	1126	17·2	2·05	1·61	1·30
1938	938	14·3	1·59	1·28	0·96
1939	1113	17·0	1·75	1·42	1·18
1944	1204	18·3	0·29	0·21	0·23

The numbers of nests have been compared with the Ministry of Agriculture and Fisheries' returns for 4 June of the previous year, proportionate adjustments being made to allow for the fact that the area under survey does not exactly follow the parish boundaries. One anomaly was immediately apparent; between 4 June 1932 and 4 June 1933 the total area of agricultural land (crops and grass) fell by about 17%; it remained sensibly constant until 1936, and then in 1937 rose to about its 1932 value, where it remained. This cannot mean that there was any real change of land use, but must indicate some changing method of filling up the Ministry's forms. No figures are therefore given for this factor. Acreage of cereals, of cereals; roots and potatoes; and of total arable land varied irregularly from year to year, though the three factors generally moved in the same direction. There is, in general, no connexion between the movements in the acreage of arable and the rook population, but the years 1936 and 1937 are 13·5% and 8·8% respectively below the average in acreage of cereals. It is possible that this was a partial cause of the fall in population in 1938. The cereal acreage in 1938 was a little above average. Further reference to this point is made below. During the war of 1939–45 there was much ploughing of grassland, and in 1943 the acreage of cereals was about seven times, and that of total arable about five times, those of the years 1933–8. The significant, but not large, increase in the number of rooks' nests in 1944 could be connected with this. In view of the supposed preference of rooks for arable land the increase might have been expected to be larger.

I pointed out in a former paper (Yapp, 1934) that there was a remarkably low density of nests on the low-lying (but not marshy) land near the Severn (9·2 nests per square mile, compared with 15·4 for the whole area), and suggested that this might be connected with the low proportion of arable land in this area. During the course of the work several new groups of nests appeared on land below the 50 ft. contour, but by 1939 the density had risen only to 11·2 nests per square mile, compared with a density for the whole area of 17·0. During the same period the acreage of cereals in the three parishes containing most of the land below 50 ft., and little above it, was nearly doubled, but the proportion of land under cereals was still much less than for the area as a whole.

In 1944, in spite of another increase in the number of rookeries on the flat land, the density had risen only to 11·6 nests per square mile, against 18·3 for the whole area. By this time the acreage of cereals in the low-lying parishes had risen to six times what it was before the war, a much greater rise than for the area as a whole. It would seem, therefore, that absence of arable is not the sole factor which keeps the rooks away from the plain.

Besides changes in land use, the factor most likely to influence numbers of birds is weather. No meteorological station is within the area surveyed, but observations for Horfield, just outside the south-eastern corner, are published in the *Monthly Weather Report*, except that this station has no returns for the year 1934. The following monthly values were plotted for each month for the years 1932–3 and 1935–9: temperature (mean minimum, absolute minimum, mean maximum, absolute maximum, earth, at 1 ft.); rainfall; sunshine. Of these eighty-four curves none resembled the population curves at all closely. No very cold winters are included in the series, and there is no evidence that winter temperatures within the range found (January mean minimum 32° F. (=0° C.) to 38° F. (=3° C.)) has any such effect on numbers as has been found by Alexander (1947) for herons. It is, however, noticeable that in 1932 and 1937, which both preceded years with low numbers of nests, the month of March was extremely cold. The *Daily Weather Report* for Cheltenham, the nearest station, shows that in 1932 the first half of the month had consistently low minima, down to 23° F. (= −5° C.), while in 1937 the cold nights were scattered from the 1st to the 29th and there was much snow and sleet. Such conditions could affect the number of nests in the succeeding year without affecting that in the current year only if they reduced fecundity and if the rook breeds in its first season. The former might reasonably be expected, but the evidence on the latter is conflicting. The statement in Witherby, Jourdain, Ticehurst & Tucker (1938) that the rook does not breed until its second year seems to be based on indirect evidence collected by Witherby (1913). It was found that birds in immature plumage in March and April had testes intermediate in size between those of breeding birds and birds in their first winter. This simply shows that breeding state and plumage are connected, and does not prove that no birds breed in their first year, for any which did would probably not be recognizable as such by their plumage. Bedford (1911) and Dunlop (1911) had previously produced some evidence of first-year breeding, and Tucker (1935) has calculated that if no rooks breed in their first year the non-breeding adults should be 25% of the total adult population, whereas the actual proportion of non-breeders seems to be only about 10%, which suggests that the majority of rooks do breed at a year old. Even if only a minority does, the effects of a cold March on the following year's nests might be as found here. It is to be noted also that if the reduced acreage of cereals has any effect on the breeding population, part at least of it must be produced within one year, as although the fall in 1936 preceded the fall in number of nests by two years, the rise in acreage in 1938 was followed by an immediate rise in nests in 1939.

ROOKERIES

Besides the possible connexion with crops or weather, the series produced some other points of interest. One of the most striking things in the actual counting was the irregular and violent fluctuations in the magnitude of individual rookeries. There is often some difficulty in deciding the limits of a particular rookery, but sometimes there is a compact group of nests, well isolated from all others, and with no outliers. There can be no doubt that in these what appears to the observer to be a single colony also appears as such to the rooks. The yearly figures for eight of these isolated rookeries, chosen at random and comprising about 40% of the whole population of the area, are shown in Table 2.

It is clear that the correlation between the series is small, and even the run of sub-totals gives a correlation coefficient with the totals for the whole area of only 0·55. This means that the causes, whatever they may be, of the annual fluctuation in the breeding population, are very uneven in their operation, and that the results of any attempt to follow the fluctuation over a number of years by counting selected rookeries, on the lines of the Index of Heron Population, would be of very doubtful validity. Variations in the Heron Index, according to the sample selected, have in fact been recognized by Alexander (1947).

Apart from its annual variation in size 'the rookery' does not seem to be so stable as is usually supposed. Of the fifty groups of nests in the area in 1933, eighteen had been abandoned by 1939, but eighteen new ones had been founded; in addition, three had had a transient existence of 3 years or less during the period. Seventeen of these twenty-one new ones were half a mile or more from any other nests. In 1944 there were eighteen new rookeries which were not in existence in 1939. Even when all allowance is made for the difficulty of delineating a rookery, it seems clear that the breeding groups are by no means firmly established. There is some indication in the detailed figures that the death-rate of a cohort (Deevey, 1947) of rookeries is independent of their age, at least after the first year or two. If this were assumed to be true, the average life of a rookery

would be 12 years, but a much longer series is needed to obtain the correct figure. The mutability of the colonies is confirmed by the detailed histories of many of those which have had a continued existence throughout the period of observation, especially those in hedgerow elms. It was exceptional for the distribution of nests amongst a group of trees to be the same from year to year. Very often one or two outlying nests, making as it were a daughter colony, would appear a hundred yards or so from the main group; in the next season the colony would have grown, and in another year or two would have completely replaced the parent. In other rookeries, especially those where the number of nests was small, different groups of trees were occupied from year to year over an area of some ten or a dozen acres. It was only in the larger rookeries (from twenty-five nests upwards), especially those in relatively isolated copses, that there was a compact and fixed grouping.

Most of the rookeries which disappeared were small, and their demise might need no other explanation than the death of all their old occupants. Some, however, were larger, and it is probable that the birds moved elsewhere. One (no. 19 in the detailed record) of 33 nests in 1933, declined steadily until it reached 5 in 1936, and in 1937 it no longer existed, while there was a parallel growth of another half a mile away; two in the grounds of Eastwood Park (nos. 40 and 41) disappeared in 1936 when the estate became the home of the Civilian Anti-Gas School. The largest of the new rookeries (no. 57) began with 6 nests in 1935, and jumped to 33 in 1936, followed by 30, 30 and 34, in 1937, 1938 and 1939. In 1944 it had 54 nests. Since the average clutch of the rook, is, according to Witherby *et al.* (1938) four, it is almost certain that the increase in 1936 was brought about by immigration. The source, however, must remain a matter of conjecture. The nearest old rookery (no. 12) was about half a mile away, and had 10, 4, and 0 nests in 1934, 1935 and 1936 respectively. It could therefore have been the home of the original founders of no. 57 in 1935, and of some of the immigrants in 1936, but is unlikely to have supplied all of the latter. All the other rookeries within 2 miles of no. 57, with the exception of one very small one, increased in 1936, and some of them considerably; the nearest group (listed as nos. 13 and 58) rose from 4 to 12 nests. It is therefore probable that most of the rooks in no. 57 in 1936 came from a greater distance, perhaps from Eastwood Park, 9 miles away, whence, as already mentioned, two well-established rookeries disappeared in that year. Since the occupants of many rookeries join together for winter roosting, it is not surprising that the breeding groups are unstable.

Table 2. *Numbers of nests in selected rookeries*

Rookery no.	Year							
	1933	1934	1935	1936	1937	1938	1939	1944
10	103	97	82	93	92	82	95	71
21	29	23	26	26	34	27	26	14
29	19	23	28	24	29	26	29	19
30	19	24	26	25	27	25	27	33
37	68	65	57	77	94	76	80	68
43	45	72	78	99	86	76	63	23
45	46	62	78	47	32	47	49	14
48	10	30	31	28	31	27	27	61
Total	339	396	406	419	425	386	396	303

ACKNOWLEDGEMENTS

I wish to thank several landowners and agents who have allowed me to visit their property; the Statistical Branch of the Ministry of Agriculture and Fisheries for supplying me with areas of crops; the Agricultural Research Council for permission to refer to the counts for 1944, which were carried out with the aid of a grant from that body as part of its Rook Investigation; and several ornithologists with whom I have discussed points arising in the work.

SUMMARY

1. Figures are given for the numbers of rooks' nests in West Gloucestershire for the years 1934–9 and 1944.

2. It is possible that the fluctuations in numbers have some connexion with the area of arable land and with the temperature in March of the preceding year.

3. A rookery is not a stable unit.

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FURTHER CHANGES IN BIRD-LIFE CAUSED BY AFFORESTATION

By DAVID and ELIZABETH LACK

Edward Grey Institute, Department of Zoological Field Studies, University of Oxford

(With 1 Figure in the Text)

INTRODUCTION

In 1922 the Forestry Commission began planting pines on the sandy Breckland heaths of East Anglia, and the consequent changes in bird-life were studied in 1931, 1933 and 1937 (Lack, 1933, 1939). To determine the later changes, we made three visits to this area in the winter of 1948–9, and others in April and August 1949, April 1950 and January 1951. The changes described previously referred to the successive stages from bare heath to dense thickets of 14-year-old pines with closely interlocked branches extending to the ground. This paper is primarily concerned with the later changes. At about the fifteenth year, the young trees are 'brashed', i.e. all the lower branches are cut off, and at the same time and at intervals thereafter, the trees are thinned out. As a result, the plantations change in character, becoming more open, with branches and needles only in the upper third of their height, and with no shrubs or undergrowth except for thin bracken, though artificial cover is provided by the brashed branches left on the ground. At 25 years old, the young pines are about 40 ft. high. The rate of growth is remarkably uniform throughout the Breckland.

The bird population was estimated by walking slowly through each plantation and recording every bird seen or heard within about 40 yards, the frequency of each species then being expressed as a percentage of all birds recorded. In 1931–7 all species, but in 1948 onward only the passerines, were included in this analysis. The percentages of passerine birds recorded in the earlier years have here been recalculated on the same basis. This method gives the relative frequency of each species, and demonstrates the changes that occur. Total censuses would be better, but they are impossible at the thicket stage of the plantations and extremely difficult later.

Full details of the counts summarized here and other unpublished material on the birds of the forests have been deposited at the Edward Grey Institute, Oxford.

BREEDING POPULATION

The changes in relative frequency of the breeding species as the young pines grow up are summarized in Table 1, in which the counts made in all years and in plantations of all ages have been combined. The changes in the three most prominent species are also shown in Fig. 1. One particular area, Wangford Warren, was counted in 1931, 1933, 1937 and 1949, and the results in Table 2 show that the general averages in Table 1 apply also to a particular area in successive years.

As a result of planting, each area passes through three main stages: (i) heath, (ii) scrub, (iii) trees, and the passerine birds fall into three main groups which change correspondingly.

The heathland birds become very uncommon after the 8th year and then disappear. Skylark (*Alauda arvensis*) and meadow pipit (*Anthus pratensis*), which are the commonest species on the heaths, still form 77% of the passerine population in 4-year-old plantations, but decrease steadily and rapidly thereafter. The much scarcer yellow wagtail (*Motacilla flava*) and wheatear (*Oenanthe oenanthe*), which form about 2% on the heaths, decrease similarly. Whinchat (*Saxicola rubetra*) and stonechat (*S. torquata*) frequent rather taller heathland vegetation than the other species: indeed they are relatively commoner in plantations 4–5 years old than on the bare heaths, but they decline rapidly thereafter.

The scrub birds are rare on the heaths, become common in the young plantations, but disappear abruptly when brashing removes the lower cover. The commonest is the willow warbler (*Phylloscopus trochilus*), which forms as much as half the passerine population in plantations 7–12 years old. Brashing causes it to disappear completely except occasionally at the edge of a plantation or where a thorn bush or young pine has grown up. In a few areas left unbrashed it also decreased after the 14th year, as the lower branches of the pines decay with time, but under such conditions the decline is more gradual. The scarcer whitethroat (*Sylvia communis*) varies in status like the willow warbler, and so does the yellowhammer (*Emberiza citrinella*), which after the 10th year persists chiefly at the edges of plantations. The last two species frequent rather lower scrub than three others, the dunnock (*Prunella modularis*), blackbird (*Turdus merula*) and song thrush (*T. ericetorum*), which are absent from heathland, reach their peak about the 10th year, and remain frequent until their abrupt disappearance after brashing.

Table 1. *Breeding population in plantations of different age*

(Percentage of population formed by each species; × means present but less than 0·5 %.)

	Age of plantations (years)											
	Un-planted heath	Scrub								Trees		
		4	5	6	7	8	9	10	11–12	14–15	18–19	23–24	26–27
Heath birds:													
Alauda arvensis	52	47	32	33	11	9	1	×	.	.	.	.	.
Anthus pratensis	27	29	31	19	5	9	1	1	.	.	.	.	.
Motacilla flava	1	.	1	1	1	.	1	.	.	.	.	.	.
Saxicola rubetra / *S. torquata*	14	19	16	9	6	7	2	×	1	.	.	.	.
Scrub birds:													
Phylloscopus trochilus	×	2	12	26	47	39	51	41	46	31	3	2	1
Sylvia communis	1	.	3	4	9	11	5	7	6	×	.	.	.
Emberiza citrinella	1	2	2	3	1	2	3	5	2	.	.	.	.
Prunella modularis	.	.	.	1	6	6	6	4	9	5	×	.	.
Turdus merula	.	.	.	1	3	6	8	8	7	5	1	.	.
T. ericetorum	.	.	.	.	1	1	4	7	1	1	.	.	.
Troglodytes troglodytes	1	.	2	3	7	6	7	12	9	9	12	12	16
Tree birds:													
Fringilla coelebs	.	.	.	.	1	4	9	13	11	21	31	37	39
Regulus regulus	.	.	.	.	.	1	2	1	3	6	8	11	8
Parus ater	.	.	.	.	1	1	1	.	4	11	26	24	25
P. major / *P. caeruleus* / *P. atricapillus*	.	.	.	.	.	.	.	.	.	1	2	5	4
Aegithalos caudatus	.	.	.	.	.	.	.	.	.	×	4	.	1
Certhia familiaris	.	.	.	.	.	.	.	.	.	×	1	2	1
Garrulus glandarius	.	.	.	.	.	.	.	.	.	3	6	3	2
Erithacus rubecula	.	.	.	.	.	1	×	.	1	6	5	3	2

Notes. (1) Based on totals of 236, 129, 183, 183, 174, 192, 330, 226, 289, 535, 207, 256 and 315, from unplanted heath to 26–27 years old respectively. These totals are not comparable.

(2) Omitted were *Oenanthe oenanthe* (common on heaths with rabbit burrows but not elsewhere), *Locustella naevia* (two in 6th year) and *Phylloscopus collybita* (less than 1 % in 14–15-year old, and occasional at edges of older plantations).

Fig. 1. Changes in the population of three species as the trees grow up.
– – – – *Alauda arvensis*; —— *Phylloscopus trochilus*; —·—·—*Fringilla coelebs.*

One other species, the wren (*Troglodytes troglodytes*), lives in much lower scrub than the others. It breeds regularly in small numbers both on the denser heaths and in the young plantations, and also in the older plantations. In the latter it frequents the bracken and the brashed branches, which are left lying on the ground and retain their needles for a long time. The wren, therefore, is much less affected by afforestation than is any other bird.

The tree birds begin to appear in the 7th or 8th year after planting and increase thereafter, not being appreciably affected by brashing. The commonest is the chaffinch (*Fringilla coelebs*), which colonizes in the 7th year and increases so rapidly that even before brashing, at the 14–15th year, it is nearly as common as the willow warbler. After brashing, it is the commonest species, forming up to 40% of all passerines. The goldcrest (*Regulus regulus*) and coal tit (*Parus ater*) colonize about the same time as the chaffinch and increase in a similar way, though not becoming so abundant. The robin (*Erithacus rubecula*) is relatively most common in plantations 14–19 years old, and thereafter apparently declines; it is therefore a borderline case, perhaps better classified as a bird of tall scrub, but it seems commoner after than before brashing. As shown in Table 1, six other woodland species colonize at a rather later stage of tree-growth, but they have not become at all common by the 27th year.

Table 2. *Changes in breeding population on Wangford Warren (planted 1926)*

(Percentage of population formed by each species.)

	1931 5 yr. old	1933 7 yr. old	1937 11 yr. old	1949 23 yr. old
Alauda arvensis	40	24	.	.
Anthus pratensis	38	11	.	.
Saxicola rubetra	11	3	.	.
Phylloscopus trochilus	5	46	54	1
Sylvia communis	.	11	9	.
Prunella modularis	.	.	9	.
Troglodytes troglodytes	.	5	6	7
Fringilla coelebs	.	.	10	44
Regulus regulus	.	.	.	19
Parus ater	.	.	2	21

Note. Based on totals of 115, 37, 94 and 270 birds respectively; these totals are not comparable.

TOTAL SUMMER DENSITY

The above data are relative and do not allow for changes in the total number of birds present. The only absolute figures are the following. On British heaths the usual breeding population is 20 to 100 adult passerines per 100 acres, the density for a Breckland heath of 65 acres being 77 per 100 acres (Lack, 1933). In a 24-year-old Scots Pine plantation of 150 acres on the Breckland equipped with nest-boxes (which permits a precise count) there were 90 breeding titmice of three *Parus* species per 100 acres in the summer of 1950. The other breeding species were not censused, but on a slow walk through this area we counted 38 titmice of the three species and 59 other passerines. If this ratio is representative, the total population was about 230 adult passerines per 100 acres. A similar calculation, for 150 acres of Corsican Pine of the same age, gave 242 passerines per 100 acres. The provision of nest-boxes increases the number of tits, especially of great and blue tits (*P. major* and *P. caeruleus*), so the total breeding population in normal 26-year-old plantations is perhaps about 180 passerines per 100 acres. This is very low compared with most woods of other types, but is about three times the usual density on heathland (Lack, 1937).

In April 1949 we also recorded the number of passerines counted per hour under similar conditions in different Scots Pine plantations, and obtained figures of 47 per hour in unbrashed plantations 14–15 years old, 24 per hour in brashed plantations 18–19 years old, and 37 per hour in brashed plantations 22–24 years old (based on $3\frac{1}{2}$, $3\frac{1}{2}$ and $7\frac{3}{4}$ hr. respectively). In Corsican Pine there was a similar marked drop in the total population after brashing. This is due to the disappearance of the scrub species, especially the willow warbler, without a compensating rise in the tree species. If the density in 24-year-old plantations is 180 birds per 100 acres, and the ratio of birds seen in plantations 22-24 years old to those seen in unbrashed plantations 14–15 years old is 37 : 47 then the breeding population just before brashing may be around 225 birds per 100 acres.

As mentioned above, there is a marked rise in the population of great and blue tits, and a smaller rise in the coal tits, if nest-boxes are set up in the plantations, which are devoid of natural holes in the trees. The population is also denser wherever thorn bushes

have been left, or where there has been underplanting with broad-leaved trees. The presence of even one or two broad-leaved trees or bushes is likely to bring in the robin, willow warbler and chiffchaff (*Phylloscopus collybita*), and occasionally other species such as blackcap (*Sylvia atricapillus*) and marsh tit (*Parus palustris*), while the typical conifer birds are also commoner there. When walking through the plantations in spring, one is immediately aware that one is near some broad-leaved bushes by the increase of bird song. Underplanting therefore achieves its intended effect of increasing the amenity of the plantations. It also emphasizes the general paucity of bird life in the conifer plantations, though this paucity has been exaggerated.

chaffinches (also most blackbirds and song thrushes) have moved out of the plantations to other habitats. As the trees grow up, the winter bird population changes in composition in a similar way to that of the breeding season, the heathland species being replaced by the scrub species and these in turn by tree species. In studying Table 3 it should be noted that the apparent increase of the wren in the scrub stage is mainly relative, owing to the scarcity of other species at this stage. The apparent decrease of the goldcrest in the oldest plantations is also mainly relative, owing to the increase in titmice as the trees get larger.

The total numbers seen per hour in Scots Pine in January 1949 were 35 in unbrashed plantations 14–15 years old, 49 in brashed plantations 18–19 years old,

Table 3. *Winter population in Scots Pine plantations of different age*

(Percentage of population formed by each species; × means present but less than 0·5 %.)

	Unplanted heath	Age of plantations (years) 4–5	6–7	8–9	10–12	13–14	17–18	21–23	25–27
Heath birds:									
Alauda arvensis	18	6	.	.	.	.	.	.	.
Anthus pratensis	48	22	2	.	.	.	.	.	.
Saxicola torquata	8	10	.	.	.	.	.	.	.
Scrub birds:									
Prunella modularis	.	.	11	8	5	2	.	.	.
Turdus merula	.	.	4	.	3	2	.	.	.
Troglodytes troglodytes	24	38	49	21	12	10	5	3	4
Tree birds:									
Regulus regulus	.	6	13	13	30	41	42	31	29
Parus ater	.	2	18	46	31	27	23	29	28
P. caeruleus	.	.	2	6	7	10	22	24	21
Aegithalos caudatus	.	.	.	.	.	.	.	6	8
Certhia familiaris	.	.	.	.	2	1	5	3	4
Erithacus rubecula	.	.	.	3	2	5	1	×	×

Notes. (1) Based on totals of 66, 50, 55, 127, 123, 300, 313, 753, and 940 from unplanted heath to 25–27 years old respectively. These totals are not comparable.

(2) Omitted were *Emberiza schoeniclus* (under 3 % on heaths and in 6- to 9-year-old trees, 16 % seen in 4- to 5-year-old trees, but almost certainly atypical); *Pyrrhula pyrrhula* (7 % in 10- to 12-year-old trees—wandering flock); *Garrulus glandarius* (2 % in 13- to 14-year-old trees, occurs at less than 1 % in older trees); *Parus atricapillus* (occasional from 8th year, 2 % in 20- to 26-year-old trees); *Parus major* (occasional from 9th year, nearly 1 % in 20- to 26-year-old trees); *Dryobates major* (very occasional in older trees).

WINTER POPULATION

The method of counting in winter was very similar to that of summer, but the large mixed flocks of titmice introduce a complication. The observer cannot identify specifically every bird in a large flock, and the method adopted was to identify as many as possible, to assume that the proportions counted were representative, and to multiply by the total number in the flock. The winter counts, combined for all years and plantations of all ages, are shown in Table 3.

Fewer species are present in winter than summer, the migratory warblers have left England, while the

and 70 in brashed plantations 22–24 years old (based on counts of $3\frac{1}{2}$, $3\frac{1}{2}$ and $7\frac{1}{2}$ hr. respectively). Comparable counts in Corsican Pine also showed a gradual increase in the bird population with increasing age of trees. Hence in winter, unlike summer, the bird population of the plantations does not decrease when they are brashed. This is because scrub species (including the willow warbler) are very scarce or absent in winter. Indeed the scrub stage of pines is almost devoid of birds in winter. The density on the heaths is also low in winter.

Underplanting the pines with small deciduous broad-leaved trees has no appreciable effect on the bird-life in winter, but the occasional thorn-tree often

brings an additional robin or blue tit, and occasionally other species.

AUGUST POPULATION

Counts made in August show that the birds are by then distributed as in winter. Nearly all the chaffinches have left the plantations and many blue tits have arrived. The goldcrest seems relatively much less common in August than in either winter or summer, presumably merely because it is much quieter and less conspicuous (see Table 4). In August a small number of willow warblers and chiffchaffs and an occasional spotted flycatcher (*Muscicapa striata*) enter the plantations and join up with the tit parties.

The objection to timed counts is that the number of birds seen and heard per hour during a slow walk varies greatly with the weather, the time of day and the observer. More birds are seen in clear sunny weather than in overcast, windy or wet weather, and more in the first hours after dawn than later in the day. Further, different observers vary, both in their speed of walking, in the distance at which they see and hear birds, and in judging whether a bird is or is not close enough to be included. In winter there is further possible individual variation in assessing the size and composition of mixed tit flocks which cannot be counted precisely. All these variations can, however, be allowed for by the procedure adopted. One of us counted for a fixed period in a Scots Pine plantation

Table 4. *Timed counts in Scots and Corsican Pine*

(Number of birds seen per hour; × indicates less than 0·5 bird per hour.)

	Apr. 1949		Aug. 1949		Jan. 1949		Jan. 1951	
	Scots	Corsican	Scots	Corsican	Scots	Corsican	Scots	Corsican
All passerines	39	35	75	46	70	27	30	48
Fringilla coelebs	14	15	1	×	.	.	.	.
Regulus regulus	4	9	5	7	19	16	8	18
Parus ater	9	4	24	18	17	5	10	12
P. caeruleus	×	×	26	10	22	1	3	1
P. atricapillus	×	.	2	×	2	.	1	×
P. major	2	.	3	2	×	.	×	×
Aegithalos caudatus	×	1	5	1	6	2	3	14
Certhia familiaris	1	2	3	4	2	3	2	3
Troglodytes troglodytes	5	1	4	1	1	×	2	1

Note. Based on simultaneous counts in Scots and Corsican Pine plantations 23–27 years old, near Swaffham, Cockley Cley, Dack, Wangford Warren and Thetford Golf Course, for 7¾ hr. in April, 14 hr. in August, 7½ hr. in January 1949 and 9 hr. in January 1951.

The totals for all passerines do not quite correspond with those for individual species, as results are expressed to the nearest individual bird, and a few very scarce species were omitted.

COMPARISON OF SCOTS AND CORSICAN PINE

The above data refer to Scots Pine (*Pinus sylvestris*). There are also extensive plantations of Corsican Pine (*P. laricio*) on the Breckland. Both species grow well there. The Corsican Pine grows slightly faster, provides denser leaf cover and has longer needles, while the undergrowth beneath the trees is much sparser. It is believed that the native Scots Pine supports a more abundant insect fauna than the introduced Corsican species, but this has not been measured. The bird-life shows certain differences.

Accurate large-scale censuses are impossible in the plantations, but when only two areas are to be compared, it is possible to improve on purely relative counts of the type shown in Table 1, by making simultaneous timed counts by two observers. and the other counted simultaneously for the same length of time in an adjacent Corsican Pine plantation of the same age. On some day later in the same week, each made a count in the area previously counted by the other. The results obtained by this means for the various plantations have been averaged in Table 4.

Table 4 shows that the chaffinch was approximately as common in Scots as in Corsican Pine, but that most other birds favoured one or other species of tree. Titmice of the genus *Parus* were normally much commoner in Scots than Corsican Pine, this always applying to the blue tit, willow tit and great tit, and usually applying to the coal tit. The longtailed tit (*Aegithalos caudatus*), on the other hand, was sometimes commoner in Scots and sometimes in Corsican Pine. The goldcrest was usually much commoner in Corsican than Scots Pine, the apparent exception in January 1949 probably being false, as our unpublished

counts in December 1948, only a month earlier, showed it to be commoner then in Corsican. The tree creeper was slightly commoner in Corsican than Scots. The wren, which depends on the undergrowth, is much commoner in Scots than Corsican, but is regular in Corsican in the few places where undergrowth is present.

SEASONAL DIFFERENCES

The number of birds recorded on a timed count depends so greatly on the degree of activity of the birds, including their calling, that comparisons should not be made between timed counts made at different times of the year. It seems reasonable, however, to compare the counts made in January 1949 with those made in January 1951. Our counts in Table 4 show that the titmice population of Scots Pine plantations in January 1951 was only about a third of that in 1949. Blue tits were particularly affected. Coal tits were also scarcer in 1951 than in 1949, but in Corsican Pines they were rather commoner in 1951 than in 1949. Longtailed tits were also scarcer in Scots Pines in 1951 than 1949, but they were so much commoner in 1951 than in 1949 in Corsican Pines, that their population on the Breckland as a whole was probably higher in 1951 than in 1949.

In the winter of 1950–1 blue tits were unusually scarce in Oxford gardens (J. Gibb, unpublished). Hence the decline in the numbers of blue tits wintering on the Breckland may have been due to factors working outside this region. The differences in other titmice suggest that, in addition, insect life may have been less abundant than usual in the Scots Pine plantations.

OTHER WINTER COUNTS

In the winters of 1948–9 and 1949–50, we visited various other State forests. The results are set out in Table 5 on a percentage basis, with totals seen per hour at the foot of the table. As the counts were taken in different weather conditions, the numbers seen per hour are not strictly comparable, but the smaller totals in Corsican Pine and Douglas Fir than in Scots Pine and Norway Spruce confirm our general impressions in the field.

Table 5. *Winter populations in conifer plantations 17-26 years old*

(Percentage of population formed by each species; × means present but less than 0·5 %.)

	East Anglia, Breckland.		Dorset, Puddletown.	North Wales		North Tyne,	Fife,
				Gwydyr.	Corwen.	Kielder.	Tentsmuir.
	Scots	Corsican	Mixed pine	Douglas	Spruce	Spruce	Scots
Troglodytes troglodytes	4	1	16	4	1	4	4
Fringilla coelebs	.	.	.	.	.	13	.
Regulus regulus	32	49	41	62	61	19	30
Parus ater	28	23	29	22	16	24	55
P. caeruleus	23	4	3	1	20	25	9
P. major	×	×	.	.	.	2	1
P. atricapillus	2	×	.	.	.	.	.
Aegithalus caudatus	6	15	5	.	.	.	.
Certhia familiaris	4	7	6	1	.	.	×
Erithacus rubecula	×	×	2	10	×	2	.
Total:	2019	1109	174	105	273	540	193
Time (in hours)	44½	39	4	4	6	9	3½
Total per hour	45	28	44	26	46	60	55

The counts were made in December 1948–January 1949, and December 1949–January 1950.

Note. North Tyne also included *Carduelis flammea* 4 %, *Pyrrhula pyrrhula* 2 %, *Prunella modularis* 3 % and *Emberiza schoeniclus* 1 %, four scrub species present because the trees had not yet been brashed. In one part where brashing had taken place, they were absent.

The counts relate to four species of trees and to regions varying from dry areas near sea-level in both East Anglia and Fife to wet areas slightly below a thousand feet in both North Wales and the Scottish border. Despite these differences, the bird-life was similar. Thus goldcrest and coal tit were the commonest species everywhere. The blue tit was usually the third commonest species, but was very variable, being abundant in Norway Spruce and usually in Scots Pine, but scarce in Corsican Pine and Douglas Fir. It was also scarce in mixed pine plantations in Dorset and rather uncommon in Scots Pine in Fife. In December 1949 also, we found it absent from the ancient Scots Pine forests of the Scottish

Highlands. On the Breckland, its numbers varied greatly in different winters, so the regional differences suggested by Table 5 should be considered provisional.

DISCUSSION

The changes in bird-life due to the growth of conifer plantations are not on a small scale. In the Cheviot area, for instance, about a hundred square miles of former moorland have now been planted. On the Breckland, 37,000 acres had been planted by 1939 (Macdonald, 1939). In these areas, it takes only a few years for all the heathland birds to vanish, while the scrub birds which replace them are in turn replaced after a few years by tree birds. Assuming an average density of 50 birds per 100 acres of heathland, this means that there are now about 18,500 fewer heathland birds breeding on the Breckland than were present 30 years ago, when the plantations were started. Likewise, assuming an average density of 180 birds per 100 acres of conifer plantation, there are now about 66,600 more breeding woodland birds on the Breckland than there were 30 years ago.

Bird-ringing has shown that, unless they are badly disturbed, most adult birds do not change their breeding territories from one year to another. Hence the first individuals to colonize the new plantations were probably mainly first-year birds raised somewhere nearby. The subsequent increase is attributable both to the breeding of these individuals and to further juveniles wandering in from outside.

A bird's habitat must provide it with sufficient food, suitable cover and a safe nesting site. In addition, a bird seeking for a place to breed is guided by psychological 'recognition' factors. The latter were discussed earlier (Lack, 1933), but the views there expressed have since been modified (see particularly Lack, 1944, 1947; Svärdson, 1949). The changes in bird-life as the heaths change into scrub and the scrub into trees are related to the basic biology of the birds concerned, and as it is hoped to study some of these species in detail later, discussion of the factors involved is here omitted.

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SUMMARY

1. Further changes in the bird-life of the Breckland consequent on the growth of pine plantations are described in both summer and winter, and summarized in Tables 1 and 3.

2. Various differences were found in the bird-life of Scots and Corsican Pine (Table 4).

3. The titmice population of the Breckland differed markedly in two winters.

4. The winter populations of conifer plantations in other parts of Britain are summarized in Table 5.

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SEASONAL CHANGES IN FLIGHT DIRECTION OF MIGRANT BUTTERFLIES IN THE BRITISH ISLES

By C. B. WILLIAMS

Rothamsted Experimental Station, Harpenden

(With 9 Figures in the Text)

For many years naturalists were reluctant to admit that butterflies, moths and other frail insects were capable of undertaking unidirectional 'migration' flights of hundreds of miles or more.

When the evidence of this became overwhelming, it was held that the flights were 'over-flow' movements from over-populated districts, and could not be compared with the 'real' migration of birds. True migration must consist of a to-and-fro movement of the population in one direction at one time of the year and in an opposite direction at a later season. In fact, in the north temperate areas, what was considered necessary to establish the existence of migration was evidence of a movement to the north in the spring and to the south in the autumn.

Round about the year 1920 only one butterfly was generally admitted to be a migrant in this sense: the monarch (*Danaus plexippus* L.) of North America. In this insect there was considerable evidence of a southward movement in the autumn, and slight evidence of a return movement in the spring.

In 1930, I published a book on the *Migration of Butterflies* (Williams, 1930), bringing forward evidence, of various degrees of incompleteness, for migration in over 200 species of butterflies from many parts of the world. There was also small evidence of a return flight in about half a dozen species.

Even at that date, however, there were competent entomologists who would not accept the idea that such movements were anything but exceptional outflows, without any relation to regular migration of birds. Dr A. H. Clark, one of the best of the North American lepidopterists, did not even accept the reality of the migration of the monarch butterfly till about eight years later.

Heape, in his book on *Emigration, Migration and Nomadism*, which was published posthumously in 1931, but actually written before my own book appeared in 1930, expressed fully the then prevailing view that 'to-and-fro' migration was fundamentally different in origin from overflow movements in one direction only, and that true migration was only known in one single species of butterfly—the monarch.

In 1936, Grant brought forward evidence of a northward movement of the red admiral butterfly (*Vanessa atalanta* L.) in the British Isles which lasted during May, June and July, and of a southward movement in September and October. This will be referred to again later.

In 1942, I brought forward evidence for a return flight at a different time of the year in a dozen species of butterflies and two species of moths (see Williams, Cockbill, Gibbs & Downes, 1942, pp. 240–8). The butterflies included, in addition to those mentioned above, *Phoebis sennae* L. in America, *Catopsilia pyranthe* L. in India; *Colias croceus* Fourc. in western Europe; *Kricogonia lycide* Godt. and *Ascia monuste* L. in southern North America and in Central America; *Vanessa cardui* L. in Europe; *Dione vanillae* L. in Florida; *Libythea labdaca* Westw. in West Africa; and *Danaus berenice* Cr. in Florida.

In fact I had then come to the conclusion that evidence for a return flight is found in a species as soon as close observations are made and a sufficient number of observers are available. It appears that in many cases the flight in one direction is gregarious and in large numbers, while the flight in the opposite direction is in small numbers with the butterflies flying singly. So long as we remained dependent for information on the accidental reports of field naturalists, the evidence was biased in favour of the conspicuous flights in one direction; when more careful observations were made the second movement began to be noticed.

Shortly after the publication of my book in 1930, an organization was formed in south-eastern England, largely by the energy and enthusiasm of Captain T. Dannreuther, to watch for evidence of directional movements of butterflies and other insects in the British Isles; and also to collect records of the occurrence of known immigrants in Britain even if there was no immediate evidence of directional movements. This organization is known as the 'Insect Immigration Committee of the South-Eastern Union of Scientific Societies'. Hundreds of

amateur naturalists have co-operated by sending in their observations, which are sorted and tabulated by Captain Dannreuther and later sent to this Experimental station for storage and further investigation. As a result of these activities we have now accumulated over 20,000 cards with records.

In 1938, the Leverhulme Foundation made a grant for two years to further the study of insect migration, and by this means Dr G. F. Cockbill made a very complete survey of the literature on the occurrence of migrant Lepidoptera in Britain, especially in the period 1850–1930 (Williams *et al.* 1942, pp. 105–28). In this investigation more than 20,000 records were filed.

A scale indicating numbers is added to each figure. In the preparation of the diagrams the records were arranged in chronological order starting from the centre so that records near the inside are for earlier years than those on the outside of the rosettes. A method was tried for putting a date to each arrow, but this was abandoned owing to the untidiness of the results, and the comparatively little gain. Only eight points of the compass were recognized and the very few records which were more exact, e.g. NNW. (usually from lightships) were placed on the nearest diagonal (NE., NW., SE. and SW.) as a small effort to counteract the preponderance of other records to the four main points N., E., S. and W.

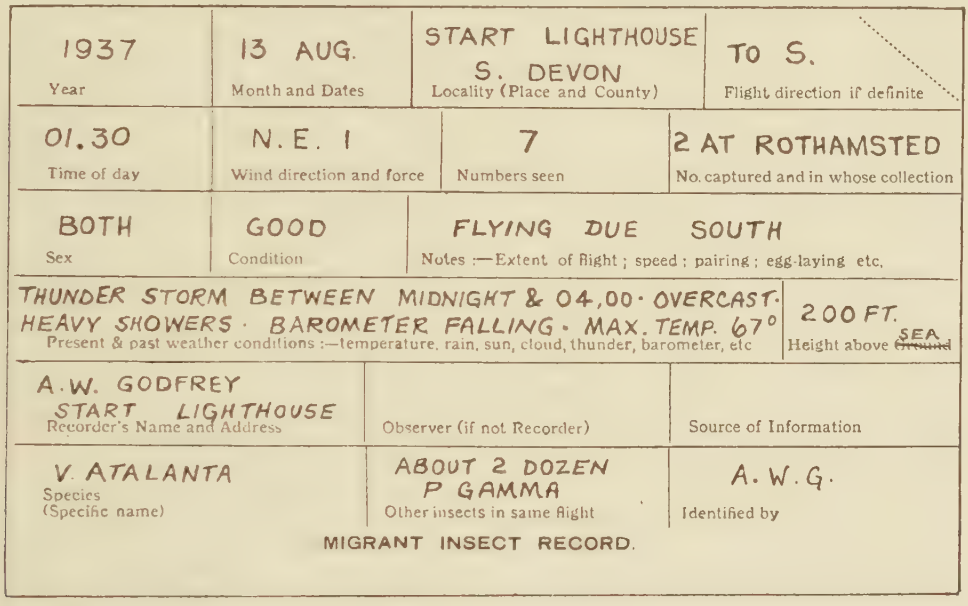

Fig. 1. Example of record of insect migration in Britain extracted on the standard card used in these investigations.

We have thus available for study a vast amount of information, mostly on standard cards of which an example is shown in Fig. 1. The cards usually give the date and locality of the observation, the number of insects concerned and the direction of flight if definite. All the cards collected in the course of our work on insect migration, including all those used for the present study, are stored in the Entomological Department at Rothamsted Experimental Station, Harpenden, and are available for inspection and study at any time by previous arrangement.

The diagrams have been prepared by the following method. Each arrow-head represents one recorded movement of butterflies and the length of the arrow represents on an approximately logarithmic scale the number of insects concerned in the flight.

The present investigations are based almost entirely on these records, and none of the conclusions would have been possible without the enthusiasm of Captain Dannreuther, Dr Cockbill, Mrs Grant (now Mrs Richardson) and the hundreds of naturalists who recorded their isolated observations.

Out of about sixty-eight species of butterflies known to have occurred in the British Isles (of which two or three are extinct or very rare) evidence for migration exists in about seventeen species. Many of these, however, are only occasionally immigrants and for them the total evidence of movement even over a long period of years is insufficient for discussion. It is in the commoner immigrants that evidence of change of direction of flight is most likely to be found. In the following pages the evidence is

discussed for six species, three of which belong to the family Pieridae, namely *Pieris brassicae* L., *Colias croceus* Fourc. and *Colias hyale* L. and three to the Nymphalidae, namely *Vanessa atalanta* L., *Vanessa urticae* L. and *Pyrameis cardui* L.

THE RED ADMIRAL BUTTERFLY

(*Vanessa atalanta* L.)

Vanessa atalanta was long considered as a permanent resident in Britain, hibernating in the adult stage in the same way as its close relatives *V. io* the peacock and *V. urticae* the small tortoiseshell. In the absence of any convincing evidence of hibernation, however, opinion changed and it was then thought to be only an immigrant from the south. Now it is considered probable that a small number of adults survive the winter, but that the majority of our summer breeding stock come in as immigrants from the south.

In 1936, Mrs K. Grant tabulated the relatively few records then available in our files relating to movements of the red admiral in the years 1934 and 1935, and showed that they indicated a preponderance of records in a northerly direction up to the end of July and in a southerly direction during September and October. In 1942, I tabulated the records for the six years 1934–9 and these supported the same conclusions (see Williams *et al.* 1942, p. 244).

Fig. 2 shows all the records that we have on our files from 1920 to 1949, classified into periods of half-months from the beginning of March to the end of November. The records vary from many referring to a single individual, to a few recording hundreds or even some thousands.

It will be seen that there are very few records in March and April, and nearly all these refer to single individuals, but even as early in the year as this there is evidence of movement in a northerly direction. In both the first and second half of May there is an increase in the number of records, with a strong northerly component. The first half of June has an unexpected number of records to the east, but in the second half of June the northerly component is again dominant. This persists into the first half of July, but by the end of this month activity seems to have died away. This is the period between the first and second broods. At the beginning of August there is renewed activity, at first chiefly in a northerly or westerly direction but after the middle of the month a definite southerly component appears and this becomes dominant during September and October, although there are flights in other directions. The frequency of observations recording a large number of individuals is much greater after the middle of August.

Our records thus support completely the earlier analyses and indicate a definite northerly movement (immigration from the south) in the spring and early summer, and a southerly movement (return to the south) in the early autumn.

THE CLOUDED YELLOW

(*Colias croceus* Fourc.)

The clouded yellow is in the British Isles a summer-breeding immigrant from the south, and there is no evidence of hibernation in any stage in this country. It is very irregular in its appearance, being in some years almost completely absent from our islands, while in other years it is abundant right up into Scotland. The year 1877, when it appeared in countless thousands all over the country, was for decades known as the 'Clouded Yellow Year'; and no similar outbreak was recorded until 1947 when it again swarmed in equal or even greater numbers. The number of records available for this latter year are sufficiently great to justify their separation into a separate analysis, which has been done below.

In 1942, (see Williams *et al.* 1942, p. 244) I tabulated records from 1931 to 1939 into two groups, those before the 15 August and those after that date. The results indicate a definite northerly movement in the first period, but movements in all directions in the second.

Figs. 3 and 4 show all our available records, with the exception of those for 1947, up to and including the year 1949, divided as before into half-month periods. Before May there are only a few records of single insects; by the second half of May, records are definitely increasing and reach a peak in June with a distinct northerly component. There is a reduction in the first half of July but with still a northerly trend, chiefly of single individuals.

Towards the end of July there is increasing activity which culminates in a great outburst of movement in the first half of August; in which, however, the northerly or westerly components are still strong: this continues also in the second half of August. By the first half of September, however, a southerly component begins to assert itself and becomes very definitely dominant in the first half of October.

Thus *C. croceus* has a northward immigration in May and June similar to *Vanessa atalanta*, but the southward autumn movement begins to show about a month later than in the red admiral. The hatching of the second brood about the beginning of August is a signal for great activity—but not for the start of the return autumn flight.

Fig. 5 shows the records of the same species in 1947, and they support the above conclusions in every possible way. There is evidence of a northerly immigration in the second half of May and the first half of June. The sudden outburst of activity at the beginning of August is again obvious: and also the

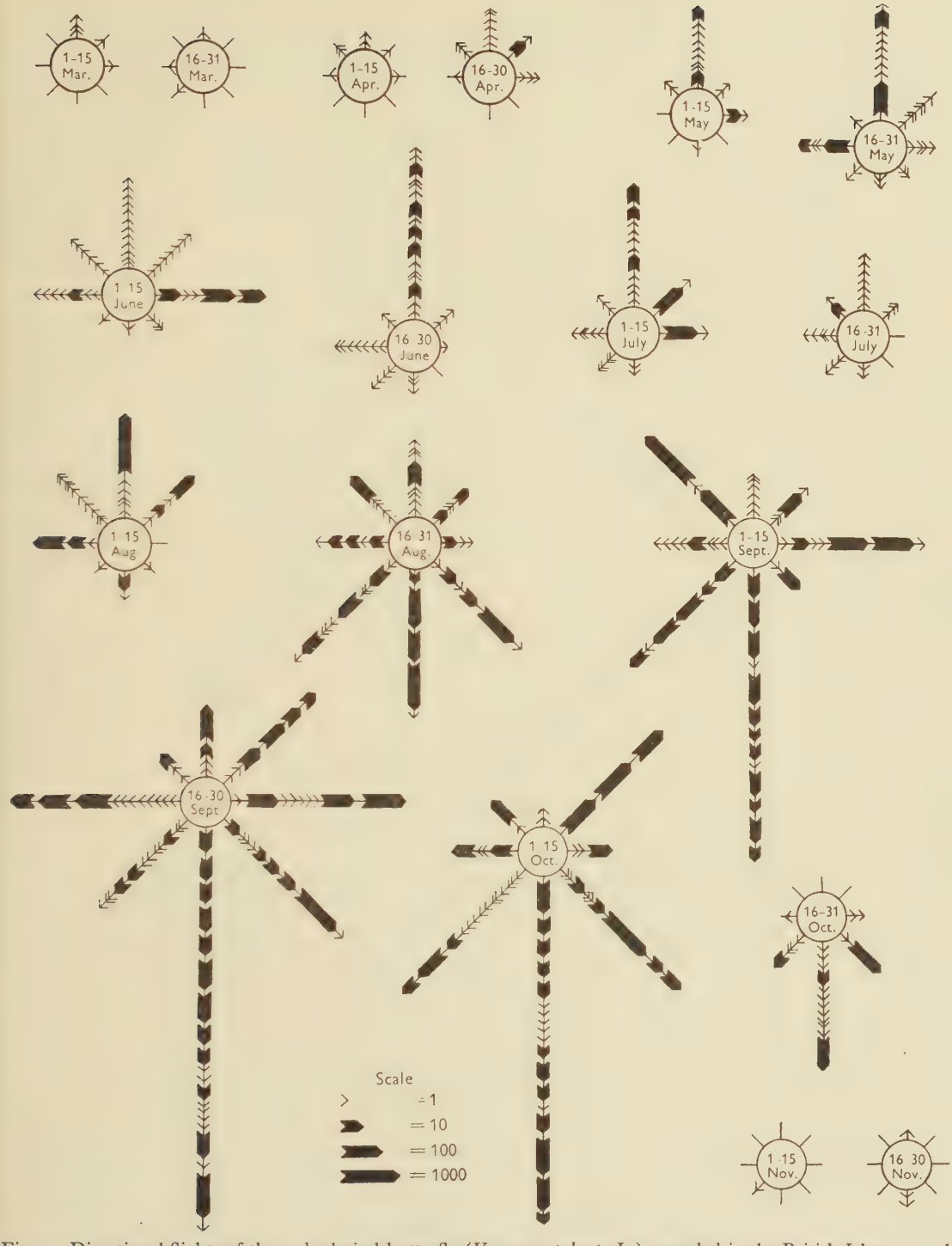

Fig. 2. Directional flights of the red admiral butterfly (*Vanessa atalanta* L.) recorded in the British Isles up to the end of 1949. Each arrow-head shows a single observed flight, the length of the arrow-head indicating approximately the numbers concerned as shown by the scale on the diagrams.

southerly autumn movement first appearing about the middle of September and becoming dominant in October. There were practically no observations in this year after mid-October.

years of comparative abundance seldom reaches as far north as Scotland.

There is also a second factor that makes the records of the species of less value than *C. croceus*, and that is

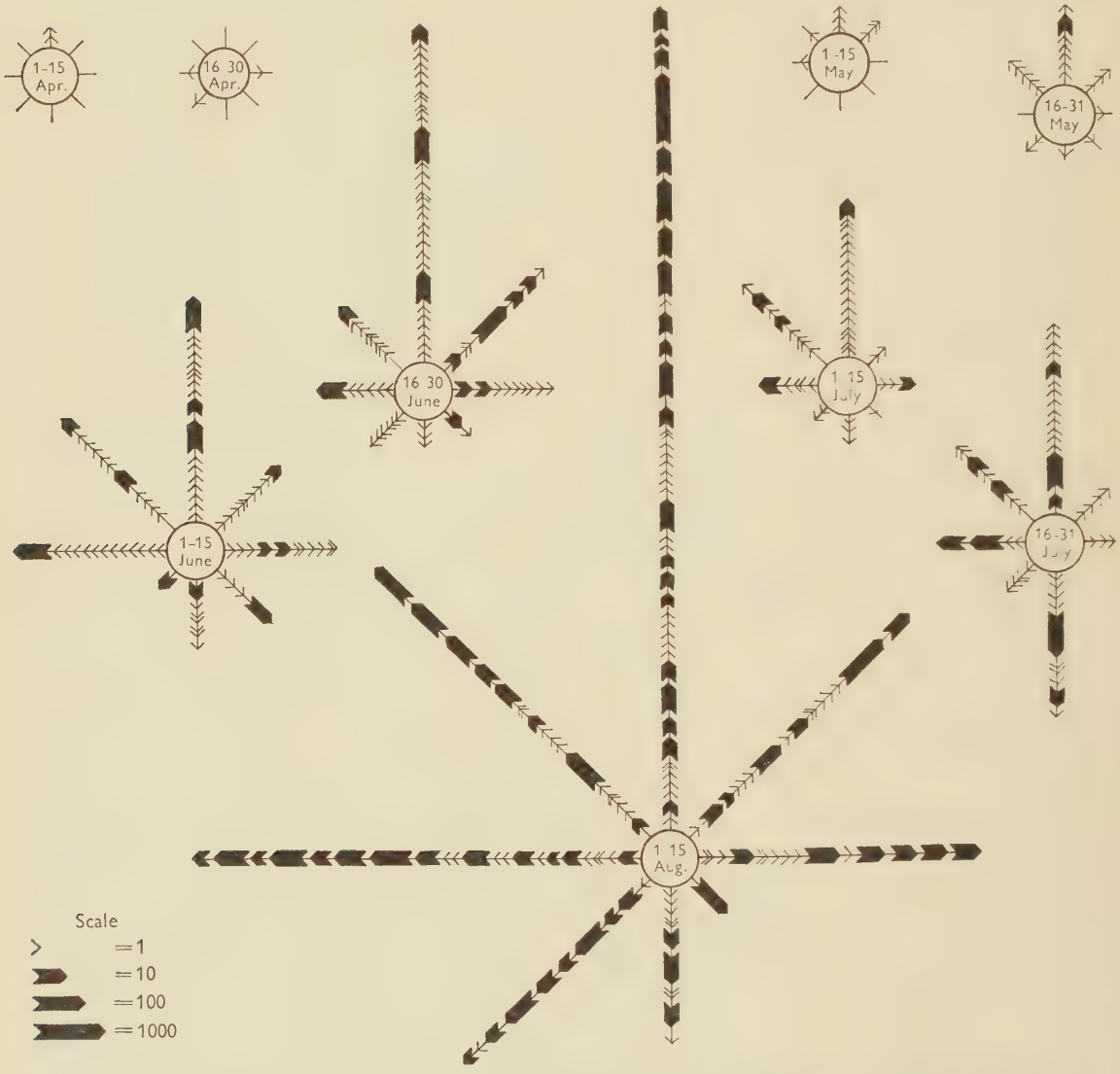

Fig. 3. Directional flights of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles up to 1949, but excluding the year 1947 (for which see Fig. 5), for the period up to the middle of August.

THE PALE CLOUDED YELLOW

(*Colias hyale* L.)

This species is a spring immigrant which comes in from the south, breeds here in the summer, but never survives the winter. Thus it resembles its close relative *C. edusa*, but is much rarer and even in its

that the latter has a pale form of the female (variety *helice*), which is in the field very difficult to distinguish from *C. hyale*, so that all records of '*hyale*' not supported by specimens are suspect.

Fig. 6 shows the small number of records attributed to this species and it will be seen that they resemble closely those of *C. edusa*. There is evidence of a small

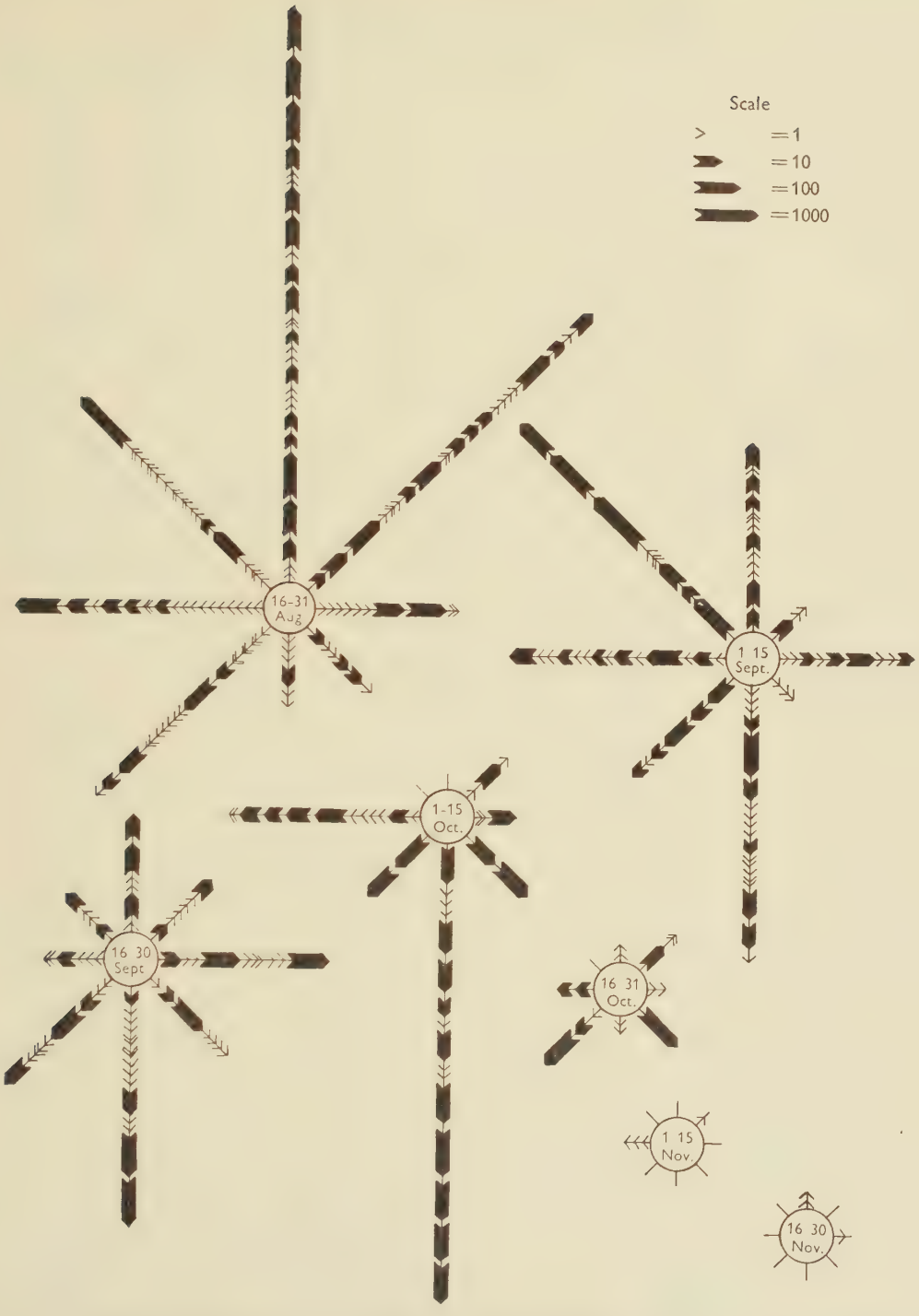

Fig. 4. Directional flights of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles up to 1949 (but excluding the year 1947) from the middle of August onwards.

immigration in the spring in a northerly direction; a period of quiescence followed by an increase of activity in August; and finally a southerly movement at the end of September and in October.

no evidence of survival in any stage in Britain during the winter.

Fig. 7 shows all the records available in our files on the same system as before. After a few wanderers in

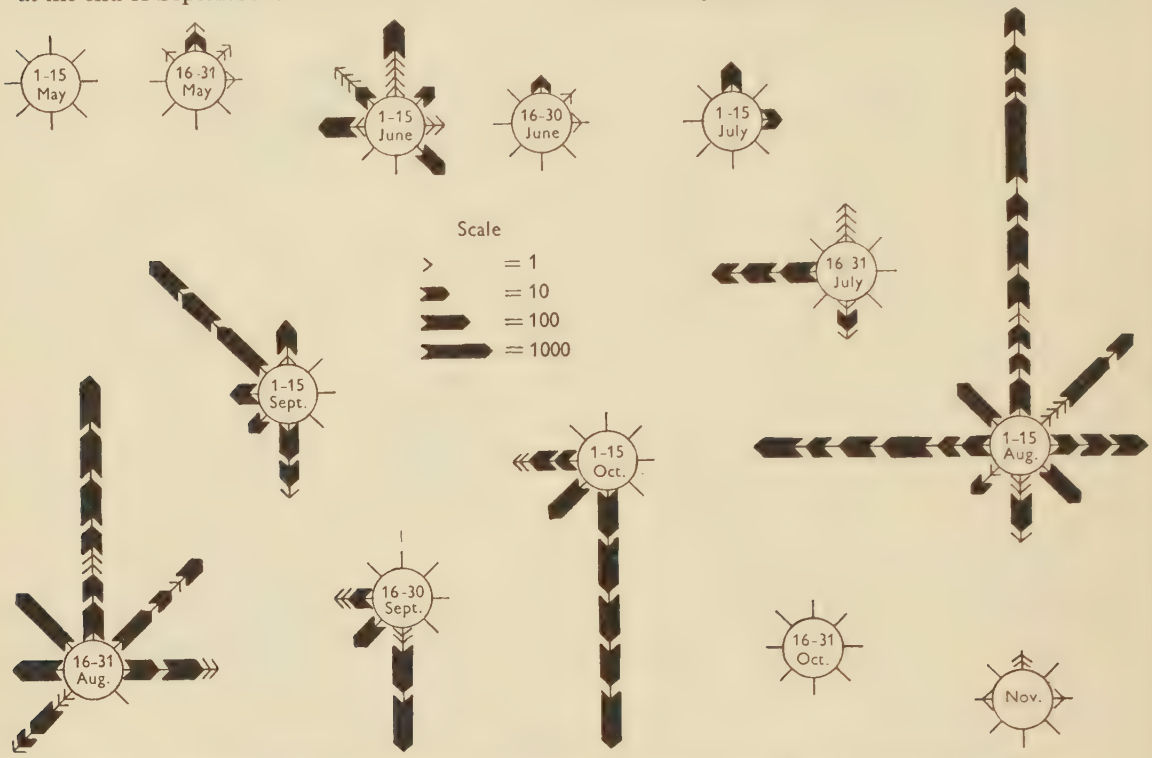

Fig. 5. Directional flight of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles in the year 1947 during the greatest immigration since 1877.

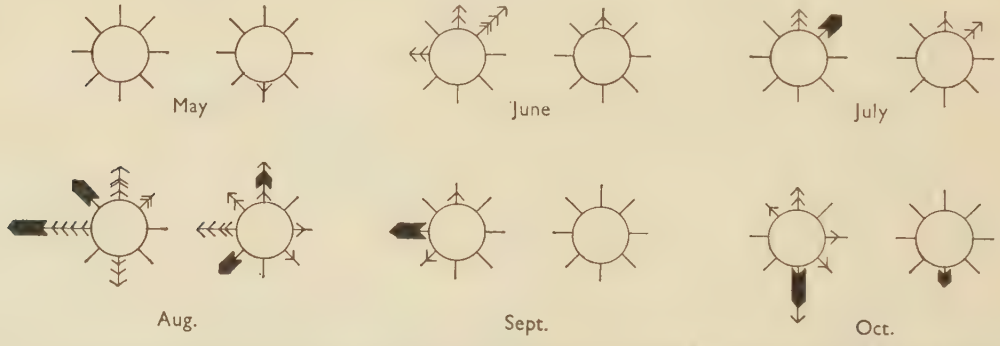

Fig. 6. Directional flights of the pale clouded yellow butterfly (*Colias hyale* L.) recorded in the British Isles up to 1949.

THE PAINTED LADY

(*Vanessa cardui* L.)

This is one of the greatest migrants in the world, and comes north to Britain from the North African area each spring in varying numbers. There is practically

early spring, the real northerly movement starts in May and reaches its peak in the first half of June. In the second half of June and in early July there is still evidence of a northerly or north-westerly movement but in reduced numbers. In the second half of July there is evidence of a westerly movement which

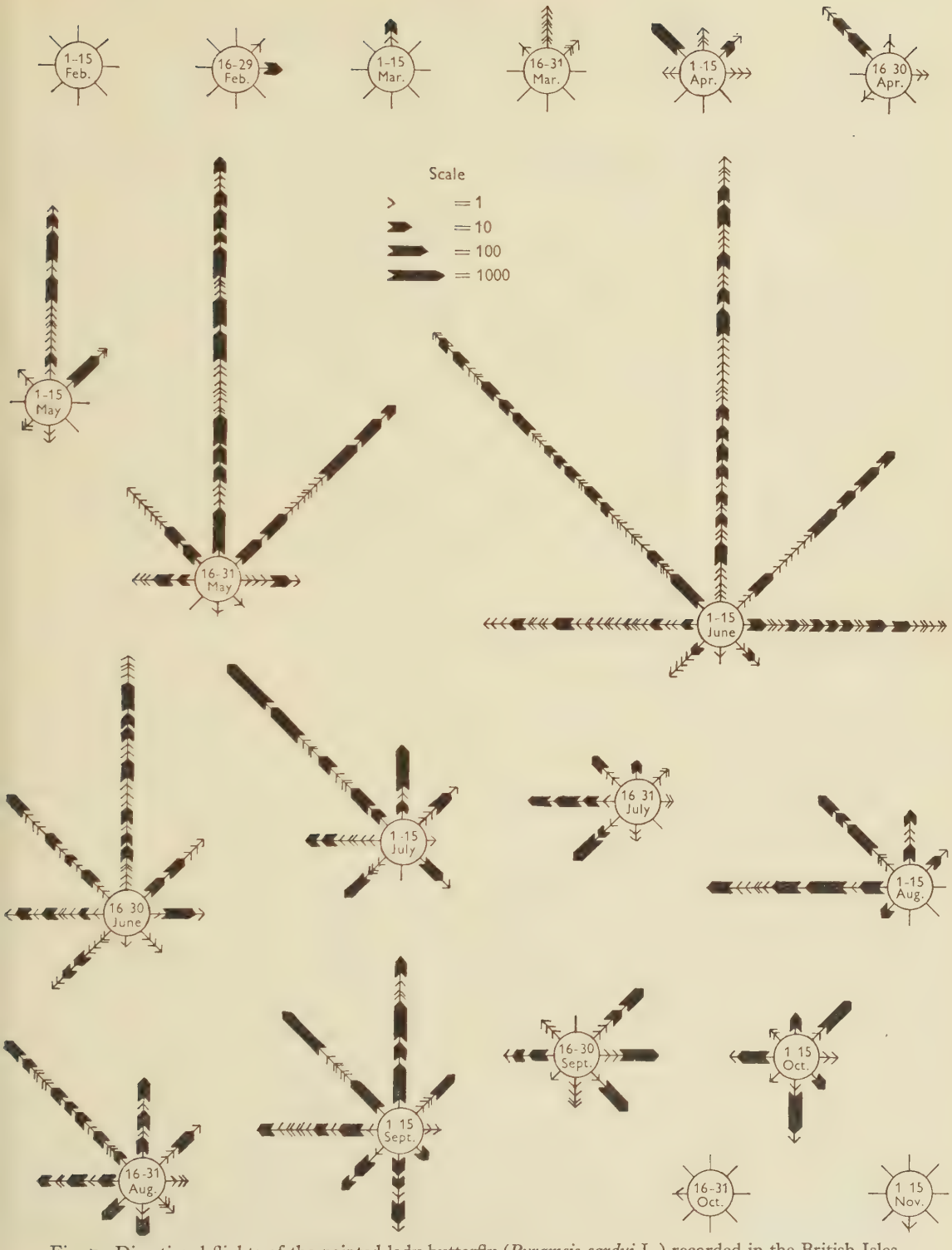

Fig. 7. Directional flights of the painted lady butterfly (*Pyrameis cardui* L.) recorded in the British Isles up to the end of 1949.

increases in August, but tends to become more north-westerly at the end of August and in the first half of September. At no period in the autumn is there evidence, from these records, of a dominant movement in a southerly direction.

This is curious and unexpected—and may be associated with the fact that there are several records of immigration into south and south-east England in the autumn from the Continent, indicating an instability of population.

THE SMALL TORTOISESHELL

(*Vanessa urticae* L.)

The small tortoiseshell butterfly has not, up to the present, been usually considered as one of our immigrant species. It is a regular hibernator and undoubtedly our population is in no way dependent on immigration for survival. On the other hand, there are a few records of directional movements on the Continent, and on twenty or thirty occasions individuals have been seen at lightships up to thirty miles or more from our south, south-east and east coasts (see Williams *et al.* 1942, p. 133).

The cards recording movement in any definite direction were comparatively few and are shown in Fig. 8 divided into three seasons. Surprisingly, they show evidence of a northerly movement in the spring and up to the end of July; and a southerly movement in the autumn, from September on. A closer watch must be kept on this species, which appears now to be an immigrant.

Fig. 8. Directional flights of the small tortoiseshell butterfly (*Vanessa urticae* L.) recorded in the British Isles up to the end of 1949.

THE LARGE CABBAGE WHITE BUTTERFLY

(*Pieris brassicae* L.)

The known movements of this butterfly (see, particularly, Williams, 1939; Williams *et al.* 1942, pp. 189–204) are very different from those of the species so far discussed. There is in central Europe a definite southerly migration about the end of July, which sometimes reaches 'snow storm' densities. Off-shoots from this stream seem to break away to the west, cross the North Sea, Holland, Belgium and northern France, and invade our south-eastern shores. There is also some evidence of an earlier migration season at the end of May. There are, quite a number of records of this in the British Isles, but comparatively few on the continent: but whether this difference is due to the relative numbers of skilled observers or to the behaviour of the butterflies cannot yet be decided.

A high proportion of our records in England relate to flights coming in from the sea along our southern and eastern coasts. As these are nearly always stated to be coming in more or less at right-angles to the coast, it was decided to divide the records into four categories: (1) flights observed well inland; (2) flights near the coast but not definitely stated to be coming in from the sea; (3) flights stated to be coming in from the sea; and (4) flights at sea recorded at lightships or from steamers in the Channel. It should be noted that estimates of actual numbers seen are less exact in this common butterfly, and flights of only a few individuals are seldom recorded. The representation of the flights on the diagram is therefore rather rougher than in the previous cases, and consists usually of 'a very few', 'dozens', 'hundreds' or 'thousands'.

Fig. 9 shows the records sorted into the four groups, as described above, and into half-monthly periods. In group 1—records inland away from the coast—there is some evidence of a northerly movement in the second half of May and first half of June; with a recrudescence of activity about the middle of July, rapidly reaching a peak and dying away soon after the middle of August. Although there are distinct southerly and south-easterly components in this second period they are by no means dominant and flights are recorded all round the compass.

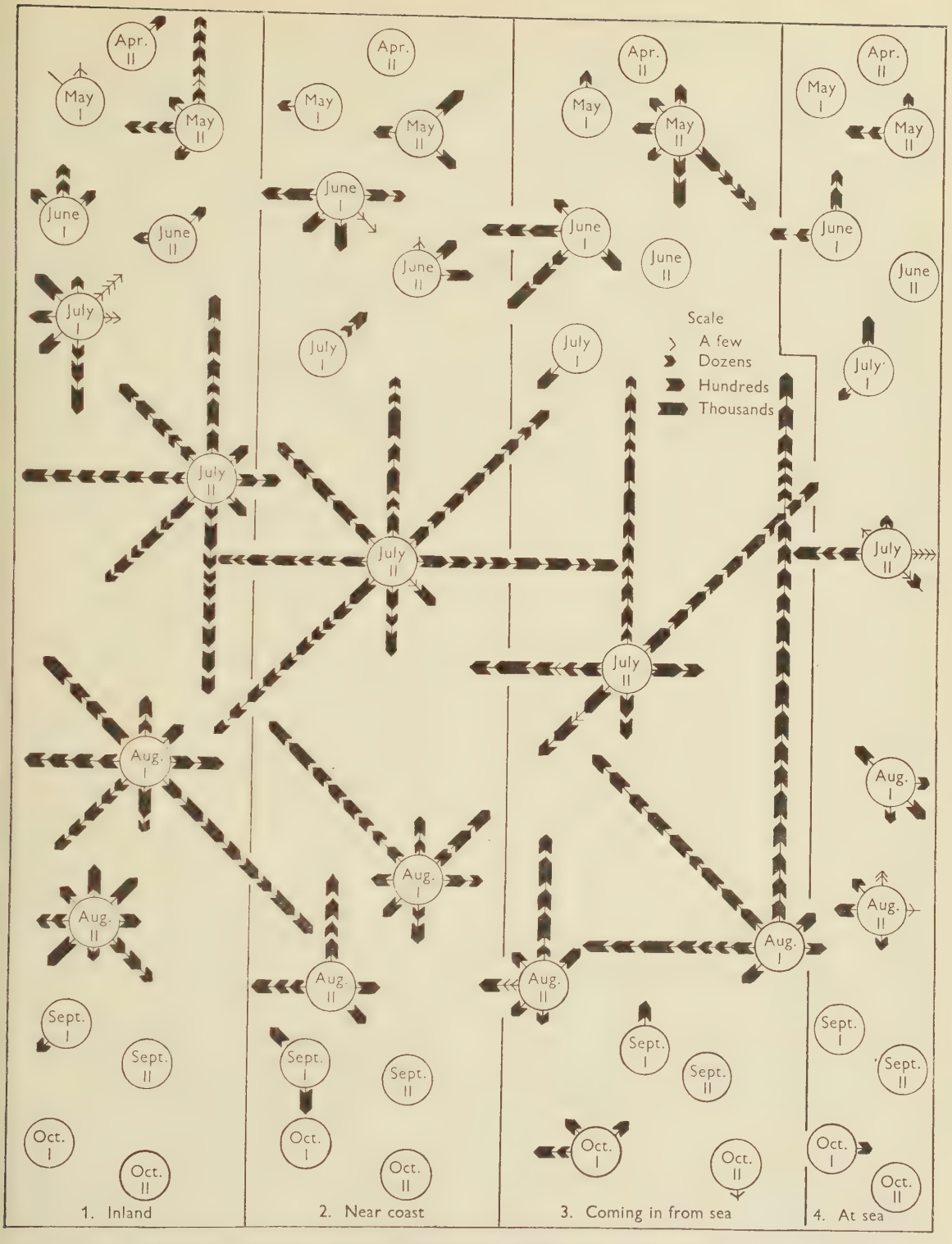

Fig. 9. Directional flights of the large cabbage white butterfly (*Pieris brassicae* L.) in the British Isles up to the end of 1949, separated according to whether the flights were observed: (1) well inland, (2) near the coast, (3) coming in from the sea, or (4) at sea.

In group 2—near the coast but not stated to be coming from the sea—there are the same two seasons, (i) end of May and June and (ii) second half of July and beginning of August, but there is no definite northerly trend in the first season and the second has scarcely any southerly component.

In group 3—coming in from the sea—there are the same two seasons, with strong northerly and westerly components in the second.

In group 4—insects observed at sea—there are very few records but some indication of a northerly trend in the first season.

The two seasons undoubtedly correspond to the first and second brood of adult butterflies.

There appears to be little doubt that the records in groups 2 and 3 are affected by the distribution of observers on our coastline. If the migrating butterflies on approaching a coast tend to fly straight in, or if observers on the coast tend to record the flights as coming directly in when the flight is really at an angle, the observations are likely to be misleading. The larger number of observers along our southern coasts, also tends to increase the number of records to the north.

Groups 1 and 4, records inland and out at sea, appear to be free from these errors, and it is curious that both of these show a northerly trend in the May-June season. There is no supporting evidence for this direction in this earlier season in the few records available from Central Europe, although they are most certainly more westerly and less southerly than the records for the later season (see Williams *et al.* 1942, p. 204).

SUMMARY AND DISCUSSION

An examination of over a thousand records of directional flights in the British Isles, relating to six species of butterflies, shows distinct evidence of a northerly movement in the spring and a southerly movement in the autumn in four species: *Vanessa atalanta*, *V. urticae*, *Colias croceus* and *C. hyale*. In *Pyrameis cardui* there is strong evidence of the northerly spring flight but the numerous autumn flights do not show any dominant southerly component. In *Pieris brassicae* there are two migratory seasons, one at the end of May and early June, and the second at the end of July and beginning of August: in the first there is evidence of a northerly movement when away from the apparently confusing effects of coast lines, but the second flight has no obvious southerly trend in Britain.

It thus appears that the analysis of numerous records of the type here available, sent in by hundreds of amateur observers, is capable of being used to demonstrate these movements, particularly when they do not occur in spectacular densities ('like snowstorm' etc.), and further that the reality of the double flight, towards the poles in the spring and towards the equator in the autumn, cannot now be questioned for a high proportion of our regular immigrants.

This brings the migratory movements of butterflies into line with the migration of birds, and partly at least disposes of Heape's physiological separation of the two types of movement which he called 'Migration' (in two directions) said to be due to reproductive influences, and 'Emigration' (in one only), due to alimentary or food impulses.

I have already (Williams *et al.* 1942, p. 250) pointed out the difficulty of accounting for the persistence of a habit of movement in one direction only on any theory of evolution. If we accept that directional movement in butterflies is simply an overflow from an over-populated area, and that none of the emigrants ever return; then the species must be perpetuated by the offspring of those individuals which do not emigrate. Thus a habit must persist for countless generations, in spite of the fact that all individuals which develop it die without contributing to the continuity of the species.

It is therefore of interest to see that the more closely the subject of directional flights in butterflies is studied, the more frequently it is found that flights in both directions exist, even if they need close observation to discover. In 1930, I wrote that the majority of butterflies seemed only to have flights in one direction, but 'whether this expresses a biological truth or is only the result of our present lack of knowledge it is impossible to say at this time' (Williams, 1930, p. 324). In 1942, I stated that the search for evidence of movement in Lepidoptera had not been carried out sufficiently thoroughly to justify a theory that required two fundamentally different origins for migration.

There is still much to be learned, but the continual accumulation of records is supporting my belief that the migration of butterflies will be found to come into line with the migration of birds, and will not contradict the fundamental theories of evolution.

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THE POLLEN COLLECTED BY BUMBLE-BEES

By ANNE D. BRIAN

Feddens, Cardross, Dunbartonshire

This study was carried out in western Scotland (Dunbartonshire) where the Bombidae, though numerous, are represented by few species. *Bombus lucorum* L., *B. agrorum* Fabricius, *B. hortorum* L. and *B. pratorum* L. are all common, the first being perhaps the most abundant. Only two other species, *B. terrestris* L. and *B. jonellus* Kirby, have been seen and these infrequently. The colonies whose pollen collection was investigated were all obtained within a radius of about a mile (National Grid reference: 26/323808). Nearly all were dug up towards the end of their season, but some that were taken early in the summer were kept in observation nests until they died out. Details of the nests are given in Table 1.

Table 1. *Details of* Bombus *colonies taken for pollen sampling*

Species	Colony no.	Year	Date nest was taken or died out	No. of cells	Queens produced
B. agrorum	1	1948	Late Aug.*	32	No
	2	1948	20 Sept.	56	No
	3	1948	Early Aug.*	*c.* 250	Yes
	4	1949	Late Aug.*	76	No
	5	1950	Sept.*	*c.* 100	Yes
B. lucorum	1	1948	Early Sept.*	250	?
	2	1948	1 Sept.	562	Yes
	3	1949	Mid-Sept.	486	Yes
	4	1949	Mid-Sept.	656	Yes
	5	1949	8 Aug.	170	No
	6	1949	10 Aug.*	470	No
B. hortorum	1	1949	4 Aug.*	191	Yes
	2	1950	Early Aug.	*c.* 100	Yes

* Nest taken early in the season and kept in an observation hive until it died out.

Two methods of pollen sampling were used. In the first, pollen loads were taken from the inside of an observation nest as the workers brought them in. This required long periods of watching to obtain even a reasonable number of loads from the small number of workers foraging, and only one nest (*B. agrorum*) was sampled in this way.

The second method involved examination of the larval meconia which, in the Bombidae, are ejected before pupation around the base of the larval cocoon. Here they remain and are later visible, each as a hard mass on the outside of a pupal cocoon. In the larger cocoons of *B. lucorum* this mass is crescent-shaped and very conspicuous. Since each pupal cell is used only once for brood rearing the associated pollen residues represent all the pollen eaten by the larva which occupied it. This method of pollen sampling has many advantages, namely, that there is no disturbance of the bees while they are working nor is any food taken from them; that nests can be taken as they are found and their examination postponed until the winter; that, if necessary, the total pollen collection for each colony can be determined; and that the diets of individual larvae can be compared.

There are two, not very serious, disadvantages of the method. First, in nests badly infested with wax moth the earlier cocoons may have been destroyed by the time the nest is dug up, though this does not usually occur until the colony has virtually finished. Secondly, the pollen grains are inevitably altered by the larval digestion and are in some cases less easy to identify than when fresh.

It appeared that none of the grains were crushed during larval mastication and digestion, but were, presumably, drained of their contents through the germinal pores. As a result of this all types of pollen grain examined had shrunk slightly, and size could not be used as a reliable means of identification. On the other hand, the markings of the exine were unimpaired and often clearer than in the fresh grain. The amount of alteration in the general shape of the grain depended upon the thickness of the exine. For example, the grains of *Tilia* and *Carduus* retained their shape unimpaired, red and white

clover grains contracted from side to side, collapsing along the furrows, while some of the thin exined grains with three furrows almost meeting at the poles were often broken into three distinct, though recognizable, parts.

The method of analysing a nest was as follows. Fifty* cells were taken at random (unless the nest retained its structure sufficiently well to warrant a more accurate study and record of the position of each cell), and placed in small glass tubes with a few drops of water to soak for 24 hr. Subsequently, by beating the cell with a glass rod, the meconium was diffused in the water and a drop of the suspension transferred to a slide, stained with basic fuchsin and mounted in glycerin jelly. From each slide a series of random microscope fields were examined until about 100 (usually more but occasionally fewer) grains had been counted and identified, some to the species, some to the genus and some only to the family. The figures for each slide were then converted to percentages. On each slide there were a certain number of fragments, considered unrecognizable, which were ignored. It is probable that more of these were derived from the thin exined grains than from the thick, thus introducing a slight bias into the sampling.

THE POLLEN COLLECTED

Table 2 gives the average percentage number of grains of each plant species for the thirteen nests examined to the nearest whole number. Considering only the five most important pollen types, Ericaceae, white and red clover, *Lotus corniculatus* and *Vicia* spp., analysis of variance, using the $\sin^{-1}\sqrt{p}$ transformation (p = percentage), showed a highly significant ($P < 0{\cdot}001$) difference in the types of pollen collected by the three bee species.

The relative importance of the different pollens depends, however, not only on the number of grains but on their volume. Thus, since the volume of a red clover grain is about fifteen times greater than that of the very small *L. corniculatus*, it is obvious that the former plant is of much more importance to *Bombus agrorum* as a source of food than the latter, despite the fact that fewer pollen grains were present. It is not easy to take this volume factor into account accurately, partly because of the unidentified grains and those identified to the genus or family only, and partly because of the difficulty of assessing the volumes of grains of such various shapes. Nevertheless, since identified grains form the bulk of the sample and the size differences are so great, the adjustment has been made and the results, shown in Table 2 (giving the percentage volume of the different pollens), almost certainly give a truer picture of the pollen collection than those based on numbers alone. The volume of each grain was worked out on the assumption that all grains are spherical, an average of length and breadth being taken for non-spherical grains (the relative volumes of the different grains are given in the column headed 'weighting factor' in Table 2). Only identified species forming 1 % or more by number of the total for any nest were included in the calculations.

When the total volume of pollen collected is considered it is apparent that *B. agrorum* collected less *Lotus corniculatus* and more red clover, *Bombus lucorum* less *Lotus corniculatus* and more Ericaceae and *Bombus hortorum* more red clover than appeared from the figures for the numbers of pollen grains only. The status of white clover pollen is also affected by the consideration of volume rather than number; it is of less importance to *B. agrorum* and *B. hortorum* but more important to *B. lucorum*.

The area from which the nests were taken is on the north bank of the Firth of Clyde. Here the land rises northwards, to 2000 ft. in about 4 miles. The flat arable fields along the shore provide little in the way of bee flowers apart from some temporary leys which include alsike and red clover. As the land rises, arable gives way to permanent pasture with abundant wild white clover and other bee plants, chiefly *Ranunculus* spp. and *Prunella vulgaris*. Higher still the grassland deteriorates to rough pasture containing much *Potentilla erecta* and merging still higher into heather moor, chiefly *Calluna vulgaris* but with several large patches of *Erica tetralix*. In the area as a whole there is a good deal of woodland, scrub and waste-land providing a varied and plentiful bee flora.

It can be seen from Table 2 that only four or five of the twenty-seven plants identified were of any real importance as pollen producers to the bumble-bees. This concentration on a few plants while collecting small amounts of pollen from a great many others was also found to be the case with honey-bees by both Percival (1947) and Synge (1947). Of the major pollen plants, considering all three bee species together, the importance of red clover is outstanding since the plant is only grown sparsely in hay mixtures and after cutting is usually grazed and flowers but little. It is almost certainly of no value to honey-bees in this area. On the other hand, it is not surprising that white clover and the Ericaceous plants, being very abundant, yielded a lot of pollen. White clover is probably the most important pollen plant for honey-bees, as well, but it is not known to what extent they collect Ericaceous pollens.

Lotus corniculatus and *Vicia* spp. (mostly *V. sepium* and *V. cracca*), though frequent along hedgerows,

* In one nest fifty cells were not available, in three others more were done before it was decided that fifty was a large enough sample.

Table 2. *Percentage of pollen grains in nests*

(The column headed *F* gives the weighting factors used to convert numbers of pollen grain

	B. lucorum								
	Nest no.								
Pollen	*F*	1	2	3	4	5	6	Av. by number	Av. b volun
Ericaceae	14	25	41	70	9	11	6	27	40
White clover	9	52	37	9	14	26	30	28	32
Red clover	29	<1	<1	2	1	<1	<1	1	2
Lotus corniculatus L.	2	11	16	11	40	7	22	18	5
Vicia L.	18	0	0	0	0	1	<1	<1	1
Tilia L.	9	1	2	4	6	5	2	3	4
Filipendula ulmaria (L.) Maxim.	2	7	1	3	15	22	5	9	3
Potentilla erecta (L.) Rausch	5	2	<1	<1	3	22	8	6	4
Digitalis purpurea L.	7	0	0	0	0	0	0	0	—
Cynareae	24	<1	<1	<1	<1	1	1	<1	1
Prunella vulgaris L.	26	<1	<1	0	0	0	1	<1	1
Rosaceae	12	<1	1	<1	3	0	18	4	6
Centaurea nigra L.	19	<1	<1	<1	<1	0	0	<1	—
Teucrium scorodonia L.	—	0	0	0	0	0	0	0	—
Calystegia sepium (L.) R.Br.	—	0	0	0	0	0	0	0	—
Succisa pratensis Moench	—	0	0	0	0	0	0	0	—
Cichorieae	—	<1	<1	<1	0	<1	0	<1	—
Umbelliferae	4	0	0	<1	<1	1	2	1	—
Plantago L.	6	0	0	<1	5	0	<1	1	1
Ranunculaceae	11	<1	0	0	<1	1	<1	<1	—
Aster L. type	—	<1	<1	<1	<1	0	<1	<1	—
Campanula L.	—	0	0	0	0	0	<1	<1	—
Chamaenerion angustifolium (L.) Scop.	—	0	<1	0	0	0	0	<1	—
Melandrium dioicum (L.) Coss. & Germ.	21	1	<1	0	<1	0	0	<1	—
Cruciferae	—	<1	1	0	1	<1	0	<1	—
Symphytum officinale L.	—	0	0	0	0	0	0	0	—
Lonicera periclymenum L.	113	0	<1	0	<1	0	0	<1	—
Unidentified	—	2	1	1	3	4	5	3	—

are nowhere very abundant, and considering the amount of pollen collected were probably much sought after by the bumble-bees. Honey-bees, on the other hand, collect hardly any pollen of *Lotus corniculatus* or the numerous species of *Vicia* with the exception of *V. faba* (Percival, 1947; Synge, 1947).

Of plants yielding small but significant amounts of pollen, *Tilia* is outstanding in view of the fact that it is not a common tree in the neighbourhood. This contrasts strongly with the honey-bee which hardly collects this pollen even when nearby. Rosaceous shrubs, on the other hand, though well represented in the area by *Rubus fruticosus*, *R. idaeus*, *Rosa* spp. and *Crataegus* sp. seem to have been rather neglected by the bumble-bees. Incidentally it was observed that *B. lucorum* workers visited the aphids on *Crataegus* in preference to the flowers. *Prunella vulgaris* was another plant which, though abundant in the permanent pastures, contributed relatively little pollen, and the same is true of *Potentilla erecta* from the rough grazing. *Filipendula ulmaria*, thistles (Cynareae), *Digitalis purpurea* and *Centaurea nigra* pollens were more probably collected in fair relation to their abundance.

All the other plants given in Table 2 provided only trifling amounts of pollen, but whereas some, such as *Succisa pratensis*, *Crepis*, *Ranunculus*, *Plantago* and *Melandrium rubrum* are frequent in the neighbourhood, *Chamaenerion angustifolium* (= *Epilobium angustifolium*) is very scarce and might well be more favoured in places where it is abundant.

DIFFERENCES BETWEEN THE BEE SPECIES

Despite a good deal of variability from nest to nest, the figures show that the habits of the three species when collecting pollen differ markedly. *Bombus lucorum* was outstanding for the collection of Ericaceous pollen. This almost certainly came mainly from *Calluna vulgaris* since, though visiting *Erica tetralix* in quantities, the bees observed on these were all collecting nectar 'illicitly' from holes bitten at the base of the corolla. Nests 5 and 6 collected little because they finished before the *Calluna* was out, but nest 4 also collected little though still flourishing in September. *Rhododendron ponticum*, the only other Ericaceous shrub growing abundantly in the neighbourhood, flowers early in the season before many workers are about and though visited freely by all species of *Bombus* probably contributed little to the Ericaceous pollen collected. Three other plants, *Tilia*, *Filipendula ulmaria* and *Potentilla erecta* were apparently only visited by *Bombus lucorum*.

B. agrorum specialized in red clover, and was the only bee collecting any quantity of *Vicia* pollen.

Bombus hortorum collected red clover even more markedly, and the absence of *Lotus corniculatus* pollen was striking. *Digitalis purpurea*, collected in small amounts, was a speciality of this species.

The position of white clover is interesting, since it is the only major pollen plant collected by all three species, though when the volumes are taken into account it appears that it was of most importance to *Bombus lucorum*. It is, of course, probably the most important pollen plant for the honey-bee here as elsewhere. Thistles (Cynareae) and *Prunella vulgaris* were the only other two pollens which, though of far less importance, were collected by all three bee species.

VARIABILITY BETWEEN PUPAL CELLS

In *Bombus agrorum* the pupal cells resulting from a single batch of eggs remain together after the adults have emerged and, since these groups of cells are arranged with the later-formed on top of the earlier, it is possible, in small nests at least, to determine the pollen intake of an individual larva in relation to time and also to that of other larvae derived from the same egg batch.

No obvious seasonal trend was found in any of the four nests in which this more detailed examination was possible. This is hardly surprising, since the four pollens chiefly concerned, red and white clover, *Lotus corniculatus* and *Vicia*, all have a long flowering period lasting through the whole season of bee activity. On the other hand, in some cases quite pronounced differences in the proportions of the various pollens were found between different groups of pupal cells. This was probably caused, not by a change in the pollens available in the field, but by the continual turnover among the foraging bees, each with its own idiosyncrasies in the matter of pollen collection.

Differences were also found between pupal cells of the same group, though these were not usually so marked as those between groups. Table 3 shows one example. These differences probably arise from the method of larval feeding adopted by *Bombus agrorum*. Although each group of larvae lie and feed on a mass of pollen common to the whole group, this pollen-mass is replenished from only two, or occasionally three, places where pollen pockets have been made in the wax covering of the larvae. Foraging bees deposit their pollen loads direct into these pockets, plastering them down on to the pollen already present. As a result, since individual workers tend to collect one type of pollen or a particular mixture for several days in succession and also probably tend to deposit successive loads in the same pollen pocket (Brian, A. D., unpublished), it is not surprising that larvae on opposite sides of the same group may receive different proportions of pollens. This provides another

Table 3. *Percentage of pollen grains in the cells derived from one group of larvae in* Bombus agrorum *nest* 1.

Cell number...	1	2	3	4	5	6
White clover	24	17	13	3	28	24
Red clover	29	10	30	10	8	45
Lotus corniculatus	5	13	47	37	3	24
Vicia	30	59	2	47	55	3

Table 4. *The number of cells in each nest containing from one to five different pollen species*

No. of pollen species in each cell represented by more than 10% of the pollen grains	*B. lucorum* nests							*B. agrorum* nests						*B. hortorum* nests		
	1	2	3	4	5	6	Total	1	2	3	4	5	Total	1	2	Total
1	12	14	47	3	2	5	83	—	3	1	6	—	10	19	19	38
2	22	18	8	11	20	17	96	6	17	6	25	7	61	19	20	39
3	13	18	5	23	18	23	100	20	21	24	33	41	139	12	11	23
4	3	—	8	12	9	5	37	4	13	18	12	2	49	—	—	—
5	—	—	2	1	1	—	4	2	2	1	—	—	5	—	—	—

variable, quality of protein, to be added to those listed by Cumber (1949) as causing the marked variation in size between bees of one egg batch.

Unfortunately, in *B. lucorum* the pupal cells fall apart so that groups cannot be recognized with certainty. Probably, however, since all pollen is fed by individual injections (Sladen, 1912), and workers feed several neighbouring larvae from a single honey-stomachful, no differences comparable to those in *B. agrorum* exist.

VARIABILITY WITHIN PUPAL CELLS

While examining the cells it was noted that, though in *B. agrorum* nests each cell contained a good mixture of the main pollen types, in *B. lucorum* cells, often one pollen-type or another would predominate. This cell composition, expressed as the number of pollen species represented by more than 10% of the grains in each cell is set out in Table 4. It can be seen that over half of the *B. lucorum* cells contained only one or two pollen species with more than 10% of the grains, but in *B. agrorum* less than a quarter. Analysis of variance showed highly significant differences ($P<0.001$) both between bee species and between nests within bee species. Although not included in the analysis the figures for *B. hortorum* show that it resembles *B. lucorum* in this respect.

This difference seems to indicate that the daily (or rather five-daily, since larvae have about 5 days of rapid growth) income of pollen to a nest of *B. lucorum* is rather more homogeneous than in a *B. agrorum* nest and might hint at some attempt at mobilization of the *B. lucorum* worker force to a particular crop. Nothing resembling the dancing of the honey-bee has been observed in *B. agrorum* (Brian, A. D., unpublished), generally considered one of the more primitive of the bumble-bees, but the matter has yet to be investigated in the more highly organized *B. lucorum*.

SUMMARY

1. Pollen collection by *Bombus agrorum*, *B. lucorum* and *B. hortorum* has been sampled by analysis of the pollen residues of larval meconia.

2. Significant differences in the pollens collected by the three species were found: *B. agrorum* collecting mainly red and white clover, *Lotus corniculatus* and *Vicia; Bombus lucorum*, white clover and Ericaceae; and *B. hortorum*, red clover.

3. Detailed analysis of *B. agrorum* nests showed no seasonal trend in pollen collection, but pronounced differences in pollen composition between different groups of pupal cells and, to a lesser extent, between cells of the same group.

4. Individual cells of *B. agrorum* were found to contain a greater variety of predominant pollen types than those of *B. lucorum* or *B. hortorum*.

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ORNITHOSIS IN CERTAIN SEA-BIRDS

By J. A. R. MILES* and J. B. SHRIVASTAV
Department of Pathology, University of Cambridge

In 1929–30, following the importation of a large number of infected South American parrots (mainly of the genus *Amazona*) into Europe, there were a large number of human cases of viral pneumonia due to infection with virus from these parrots. It was early recognized that other birds were susceptible, and it was shown that finches of both the families Fringillidae and Ploceidae were highly susceptible to infection from parrots in pet shops and that they developed a generalized disease which was almost invariably fatal (Bedson, Western & Simpson, 1930; Meyer, 1948).

Meyer & Eddie (1933) reported that infection with psittacosis virus was widespread among budgerigars in Californian aviaries, and they worked out the epidemiology of the disease in these birds. They found that a high percentage of the adult stock were carrying the virus, but that normally no virus was shed and the birds were non-infective. When the birds were subjected to bad conditions in pet shops or to the physiological stress of breeding, they could again become virus shedders and infect the young birds in the nest. Infected fledgelings showed ruffled plumage, lassitude, often a nasal discharge and a soiled vent. About 9% of such birds died and the rest recovered clinically, but remained virus carriers and were likely to pass infection to their own young in the next season. Normally the budgerigar cleared itself of virus during the second year, and although a large spleen might be present in 2-year-old birds, it was not usual to be able to isolate virus from it.

At this stage the disease was regarded as primarily one of South American parrots, and the infection of the Californian aviary budgerigars was thought to be due to infection from South American birds. Meyer & Eddie (1934), therefore, imported a stock of Australian budgerigars in the hope of obtaining a disease-free stock. These birds on arrival were found to be heavily infected, and Burnet (1934) showed that the disease was widespread in Australian psittacines.

In 1933 an epidemic of a new disease occurred in the southern part of the Faroe Islands, and the doctors on these islands then recognized that they had had a few similar cases in previous years beginning with two in 1930. The epidemic occurred in the first fortnight in September, the disease was a pneumonia and the mortality was approximately 20%. Similar epidemics followed in succeeding years. Rasmussen, a medical practitioner on the islands, recognized the similarity of the disease to psittacosis and that the epidemic followed 1–2 weeks after the fulmar fowling when young fulmars (*Fulmarus glacialis*) were taken for salting for winter food (Rasmussen, 1938; Rasmussen-Ejde, 1938). Carcasses of such birds were sent to Haagen and Mauer at the Kaiser Wilhelm Institute, Berlin, and they easily isolated a psittacosis-like virus by intraperitoneal inoculation of organ extracts from the juvenile fulmars into mice (1938).

In 1940, Pinkerton & Swank showed that a similar virus was present in certain pigeons, and since then it has been shown that a high percentage of pigeons both in America and in Britain are infected with such a virus, but its pathogenicity for mice and its infectivity for men appears to be much lower than that of the classical parrot strains of 1930 or the fulmar strains.

Virus has since that time been isolated from a number of other Columbiformes, from domestic ducks and chickens and from many other birds under zoological garden or pet shop conditions which may have allowed cross-infection. Where adequate descriptions of these viruses have been given they appear to show more resemblance to the pigeon type with low pathogenicity for mammals than to the parrot-fulmar type.

In 1947, Pollard reported on investigations of what he described as American shore birds. He found serological evidence of infection among Laridae including the herring gull (*Larus argentatus smithsoniana*) and several species of tern, and he isolated an ornithosis virus from a large sandpiper, the willet (*Catotropotus semipalmatus*).

In 1949, we had the opportunity to visit the Faroe Islands and to make some observations on the disease of the fulmar. In 1950, we looked for the disease in fulmars in Shetland and in some species of gulls in Wales. We also made serological investigations on manx shearwaters (*Puffinus puffinus*) in Wales.

FIELD OBSERVATIONS

Fulmars in the Faroe Islands

From 1933 to 1937 epidemics of 'psittacosis' occurred in the southern two Faroe Islands (Suduroy and Sandoy) every season, but only a few sporadic

* Now at the Institute of Medical and Veterinary Science, Adelaide, South Australia.

cases on the other islands. In 1938, when the aetiology of the disease had been clearly established, the taking of young fulmars was made illegal, and in the southern islands where the epidemics occurred this law has been obeyed most faithfully. In other islands a few cases have continued, although very few of the people do now take young fulmars. Haagen & Mauer had isolated virus from a pool of material collected in an area where there had been no human cases, and we were fairly confident that by 1949 the disease would be widespread among the Faroese fulmars.

Owing to circumstances in no way influenced by its suitability for the investigation under consideration we made our main centre in the Faroe Islands on Viðoy in the Norduroyar, and all our own investigations were on fulmars nesting on that island or taken on the water close to the island. We were present on the island from 7 to 28 August, during which time we were able to observe some of the nesting sites and to gain some idea of the distribution of nesting fulmars around the island. At no point was there more than a mile between nests, and the cliffs can be regarded as one large colony, but around most of the island the nests were well spread out and only on the north-east, where the cliffs are very high and supply large areas of ledges suited to the fulmar, were there very numerous nests in a relatively small space, but even in this area there was no gross overcrowding.

The local experts told us that the young birds began to leave the cliffs about 25 August, that normally most birds left in the last two days of August and the first two in September, and that sick birds were not seen on the water until early September. We were unfortunately not able to stay for the whole season during which the juveniles were leaving the cliffs and, therefore, decided to attempt three things:

(1) To examine juvenile birds in the more accessible nests on certain cliffs.

(2) To examine any juveniles which we found on the water early in the season.

(3) To examine sera from adult birds for the presence of antibodies against the virus.

On 24 August we attempted to examine young birds on the cliffs above Vidvik on the south-east of the island. The cliffs proved considerably more difficult than we had anticipated, and most of the more accessible nesting sites were already deserted when we arrived. We obtained two birds, both of which were normal, and none of the juvenile birds on the inaccessible parts of the cliff appeared to be sick.

On 26 August we collected young birds on the water. During 6 hours we collected only ten juvenile fulmars, two of which appeared to be sick. The more severely ill bird was lying on the water with wings partly extended and head down. The head and neck were fouled with fulmar oil and the bird showed a slight nasal discharge. There was no evidence of soiling of the vent. At post-mortem a small amount of fibrinous peritoneal exudate was found. The spleen was normal in size, but there was some patchy consolidation of the lungs. Histological examination of these tissues revealed the presence of the typical inclusion bodies caused by viruses of the ornithosis group (the so-called L.C.L. bodies).

On 26 and 27 August twenty-three adult fulmars were obtained on the island of Viðoy, blood was taken, a post-mortem examination was made and material was removed for attempted virus isolation. In considering the results of the first day's examinations it occurred to us that the only birds which had shown large spleens were female birds and, thereafter, we noted the sex of all birds. Of the last seventeen birds collected ten were females and seven males; of the females six showed large spleens but the males were all normal. Two of the females with large spleens gave serological evidence of ornithosis (Table 1).

Fulmars of Shetland

In the summer of 1950 fulmars were examined on Fair Isle and the small island of Colsay just off the west coast of the south part of the mainland. On the evening of 29 August the cliffs around Colsay were examined. No birds were seen on the water, but it was held that many of the juveniles had left since the previous week. None of the juveniles on the cliffs appeared ill. Seven birds were collected and examined. No gross abnormalities were discovered at post-mortem although there were substantial variations in the size of the spleen and the amount of subcutaneous fat in different birds. On the succeeding days birds were observed and captured on Fair Isle. No sick birds were seen. Four adults and eight juveniles were captured and bled from wing veins. Three further juveniles which were rather below average weight were killed and examined, but showed no internal abnormalities at post-mortem. Field observations did not suggest the presence of ornithosis in the fulmars on Colsay or Fair Isle.

LABORATORY INVESTIGATIONS

Unfortunately in both years bad weather slowed our return to the laboratory, and in each we lost all ice from the thermos flasks at some stage while they contained material for virus investigation; so that our failure to isolate virus might be due to prolonged storage under poor conditions. In the case of the

material from the Faroe Islands we have clinical and definite histological evidence that certainly one and probably a second of our juvenile birds was infected with a psittacosis-like virus, but since we failed to isolate a strain we have been unable to make a direct comparison with those of parrot or pigeon origin. We have no clinical or histological evidence of infection of the fulmars on Colsay or Fair Isle. In view of the small size of our sample and the delay in getting the material to the laboratory our failure to isolate a strain of virus is of little significance, but it may well have been due to the absence of the disease from those colonies. The most important point is that we saw no evidence of illness in any juvenile birds on either Colsay or Fair Isle.

Table 1. *Test for presence of complement-fixing antibodies against psittacosis*

Species of bird	No. of sera	No. of birds showing complement-fixing antibody of given titre						
		<1:5	1:5	1:10	1:20	1:40	1:80	1:160
Fulmar (*Fulmarus glacialis*): Viðoy	20	18	—	—	—	—	—	2
Fulmar: Shetland	12	10	2	—	—	—	—	—
Lesser black back gull (*Larus fuscus*)	15	13	1	—	1	—	—	—
Herring gull (*Larus argentatus*)	2	—	2	—	—	—	—	—
Greater black back gull (*Larus marinus*)	1	1	—	—	—	—	—	—
Manx shearwater (*Puffinus puffinus*)	24	20	4	—	—	—	—	—
Puffin (*Fratercula arctica*)	1	1	—	—	—	—	—	—

Sixteen of the sera collected from adult and four of those from juvenile fulmars captured on Viðoy were found to be in a fit state to be used in a complement-fixation test. When they were examined two of the adult sera showed high titre complement-fixing antibodies against psittacosis virus (Table 1) which certainly indicated recent infection with a related virus. These birds were two of the six females which had shown large spleens. Sera from four adults and eight juveniles from Fair Isle have also been examined. Two of the adult sera showed low titre antibodies (1:5 only) and their significance is doubtful. We have not obtained definite evidence either for or against infection of the fulmars on Colsay or Fair Isle, but we are fairly confident that if such infection does occur it is far less common than on Viðoy. For the latter island also our data is somewhat inadequate, but, since we were collecting early when sick birds are rarely seen on the water, we think that it is justifiable to say that not less than 10% of the birds show evidence of infection.

OBSERVATIONS ON GULLS

The observations on gulls were made during two periods on Skomer Island off the Pembrokeshire coast during the summer of 1950. The first period was the last week in June, when juvenile gulls were collected for attempts at virus isolation. At this time the herring gulls (*Larus argentatus*) which were breeding on the cliffs had succeeded in rearing young which were more than half fledged. The other species present, lesser and greater black backs (*L. fuscus* and *L. marinus*) which nested on the level top of the island had suffered a number of set-backs and had only a very few hatched young. Ten juvenile herring gulls were collected from one colony and ten others from areas used by only a few nesting pairs. None of these birds showed any evidence of disease, although some of the birds from the large colony were infested with Mallophaga and one carried a tick. During the second period (first week in August) adult gulls (mainly lesser black backs) were caught and bled from a wing vein. All these birds appeared healthy except for one which had blisters on the webs.

The material from the juvenile herring gulls was divided into two pools; the one from the birds from the large colony and the other from the miscellaneous birds. This material was inoculated into the yolk sac of embryonated hens eggs, intracerebrally and intraperitoneally into mice and intramuscularly into canaries. From the pool from the large colony a virus morphologically similar to psittacosis was isolated in the eggs, both directly and after one passage through the canary. No virus was isolated in the mice. The virus readily adapted to the egg, but even egg suspensions which caused specific deaths in eggs at a dilution of $1:10^{-7}$ would kill only from 10 to 30% of mice when inoculated either intraperitoneally or intracerebrally at a dilution of 1:10. This is in marked contrast to our parrot and pigeon strains.

Sera from fifteen adult lesser black back, two herring and one greater black back gulls were tested for complement-fixing antibodies (Table 1). Two of the lesser black backs showed antibodies, one to 1:5 and one to 1:20, and we regard this as strong evidence that these gulls are infected by a virus of this group. Both the herring gulls showed a titre of 1:5, but any doubts which we might

entertain from these low titres are dispelled by the isolation of virus from the pooled organs of juveniles of this species. The one specimen of serum from a greater black back did not contain any antibodies against psittacosis virus.

MISCELLANEOUS OBSERVATIONS

Twenty-four sera from adult manx shearwaters (*Puffinus puffinus*), collected for another purpose, were tested for antibodies against psittacosis and also one specimen from an adult puffin (*Fratercula arctica*). The puffin showed no antibody, but four of the shearwater sera fixed complement to a titre of 1:5, but no higher. These results are again inconclusive, but we have never seen a shearwater with a disease suggestive of psittacosis, and we and several of our colleagues have had prolonged and intimate contact with both juvenile and adult shearwaters, and we are confident that if they do suffer from a disease of this group it is not caused by a strain of virus highly infective for man.

DISCUSSION

The work of Mayer & Eddie showed that the virus of psittacosis was passed by the adult budgerigar to the young in the nest, and it is very difficult to offer any other explanation for the infection of juvenile fulmars or gulls. The young birds have little contact with birds other than their parents. Arthropod vectors have never been demonstrated for psittacosis group viruses and, in our experience, juvenile birds of these species carry remarkably few ectoparasites. We have only found mallophaga in about 10% of juvenile birds of each species and a tick on one of twenty gulls examined closely. The trombiculids which are so common around the vent of the juvenile shearwater, we have not found in juvenile gulls in the same areas. The areas in which we have examined fulmars appear to be singularly free from mites.

The high titre complement-fixing antibodies obtained from two adult fulmars strongly suggest that these birds had had recent contact with active virus. Low titres (e.g. 1:20) would indicate either past infection or recent infection in which antibody had not yet developed. (Our experience suggests that pigeons take 3–5 months from the time of infection to develop high titre antibodies.) In the numerous cases with fixation at a dilution of 1:5 only the result is of very doubtful significance. We regard the high titre antibodies in these two cases as confirmation of the theory that adult fulmars may carry the virus when they are present at the nesting sites. If this is so, it is interesting that birds which probably do not breed until their third season or later should continue to carry the virus long enough to infect their own young, when the budgerigar usually clears itself of infection during its second season, but it is possible that the active recrudescence of infection during the physiological stress of breeding acts as an additional stimulus to the defence mechanisms necessary if the bird is to become completely clear of the infection.

For the reasons described earlier, we have not succeeded in isolating a strain of virus from fulmars and have to rely on the report given by Haagen & Mauer of the strains which they isolated from birds sent from the Faroe Islands. These strains were highly pathogenic for mice when material from the birds was inoculated intraperitoneally. Such high pathogenicity by this route has only otherwise been reported of the 1929–30 parrot strains. The strain which we have isolated from the herring gull is of lower pathogenicity for mice than any other virus of the group of which we have had experience or have seen described. Our own pigeon strain which has been recently isolated has an intracerebral average lethal dose (A.L.D.) for the mouse not very different from that for the embryonated hen's egg. Our gull strain requires at least 10^6 egg A.L.D. to kill mice after intracerebral inoculation. The pigeon strain as well as the gull strain has a rather low pathogenicity for mice by the intraperitoneal route. We tentatively suggest that the pathogenicity of strains for mice may give some indication of their infectivity for man.

We have little evidence about the origin of the gull strain, but our incomplete investigations suggest that it is substantially different from any other strains previously isolated. Further, we have evidence that both the species on which our investigations were at all adequate were infected, and Pollard (1947) has given evidence of widespread infection of Laridae in America with viruses of this group. The unusual character of our strain of virus, together with the evidence of the infection of numerous species of Laridae in widely separated areas, leads us to the conclusion that ornithosis viruses are old-established parasites of this family.

The history of the fulmar strain is fuller and perhaps worthy of brief consideration. Colonies of fulmars have existed on St Kilda and the Westmann Islands (Iceland) from time immemorial, and the human inhabitants have always taken large numbers of young for food. Fulmars colonized the Faroe Islands between 1816 and 1839 (Fisher & Waterston, 1941) and, up to the time that taking the young birds was made illegal, around 100,000 were taken each year. The disease in man first occurred in the Faroe Islands in 1930, the year following the importation of large numbers of infected parrots to Europe, and the first epidemic occurred in 1933.

Many of the infected parrots died on the voyage and were thrown overboard in European waters where, undoubtedly, if fulmars had found them they would have eaten them. The disease was never recorded on St Kilda up to the time of the evacuation in 1931, although approximately one-half of the juveniles were taken for food each year. In the Westmann Islands the first cases occurred in 1938 and there was an epidemic in 1939 after which the taking of young fulmars was made illegal. If the disease were an old-established disease of the fulmar, one would expect it to have been evident in the old colonies first and then to have reached the new, but the evidence which we have suggests that the disease started in the recently colonized Faroe Islands and spread to Iceland 8 years later. The evidence further suggests that the rate of infection in the Faroe Islands was in 1949 much higher than in 1938 and that infection was more widespread, but we have no evidence that the disease has yet reached the large colonies now present in Shetland.

Haagen & Mauer did not investigate their fulmar strains of virus very fully, but in mouse pathogenicity as well as in their remarkable infectivity for man they appear to resemble the 1929–30 parrot strains rather than any other. All this evidence makes us accept the hypothesis originally put forward by Rasmussen that the fulmar strain of virus was obtained by feeding on the corpses of infected parrots. The weakest link in our argument lies in the occurrence of two cases of pneumonia, retrospectively diagnosed as psittacosis in Suduroy in 1930, at a time when one would expect the rate of infection among the birds to be very low; but, even assuming that this retrospective clinical diagnosis is correct, we do not think that it counterbalances the weight of evidence on the other side, especially when the first epidemic occurred in 1933 after there had been time for the rate of infection in the birds to build up.

At present we have no evidence that viruses of this group are playing any significant role in population control among the sea birds which we have examined. The virus appears normally to cause only mild disease in fulmars although, apparently, a few deaths occur. But if, as we think, this is a new infection in a rapidly increasing population, serious epizootics are possible.

In 1934 the parrot strains in Australia appeared to be behaving in precisely the same manner, but in 1938 a severe epidemic occurred among adult parrots with a high mortality (Burnet, 1939). Possibly this was due to a highly virulent mutant arising in an area with a very large susceptible parrot population. Neither in fulmars nor in gulls does the virus appear to infect a very high proportion of the population and, particularly in the case of the fulmar where there is a rapidly increasing population, it appears quite possible that a similar virulent mutant might arise and become an important factor in population control.

We wish to express our thanks to Mr James Fisher and Dr R. K. Rasmussen for much valuable information, to Dr H. D. Joensen for permission to investigate juvenile fulmars on Viðoy and to Messrs R. Codd, J. Collison-Morley, T. Henderson, H. A. Leney and K. Williamson for very valuable co-operation.

SUMMARY

1. Field and laboratory investigations for the presence of ornithosis in certain sea birds are described.

2. Evidence of recent infection in adult and juvenile fulmars (*Fulmarus glacialis*) from Viðoy in the Faroe Islands is given.

3. No clear-cut evidence of infection has been found in fulmars on Shetland.

4. A strain of ornithosis has been isolated from juvenile herring gulls (*Larus argentatus*) and serological evidence of infection found in the lesser black back gull (*L. fuscus*) on Skomer Island (Pembrokeshire).

5. No definite evidence of infection was found in sera from manx shearwaters (*Puffinus puffinus*) on Skomer Island.

6. The significance of these results is discussed, and evidence brought forward to suggest that these infections are old-established in the Laridae, but probably arose for the first time in the fulmars around 1930.

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THE LENGTH-WEIGHT RELATIONSHIP AND SEASONAL CYCLE IN GONAD WEIGHT AND CONDITION IN THE PERCH (*PERCA FLUVIATILIS*)

By E. D. LE CREN

Freshwater Biological Association, Ambleside, Westmorland

(With 8 Figures in the Text)

CONTENTS

	PAGE
1. Introduction	201
2. The analysis of length-weight relationship and condition	201
3. The length-weight relationship	
(*a*) Sources of material and methods of collection	205
(*b*) Analysis of data	205
(*c*) Results	207
(*d*) Discussion and conclusions	209
4. The seasonal cycle in gonad weight and condition	
(*a*) Gonad weight	209
(*b*) The weight of stomach contents	212
(*c*) Condition	212
(*d*) Individual variations in relative condition and gonad weight	213
(*e*) Discussion of the seasonal cycle	216
5. Acknowledgements	218
6. Summary	218
References	218

1. INTRODUCTION

The present paper is an account of some of the investigations on the biology of the perch (*Perca fluviatilis* Linn.) in Windermere, which are being conducted in connexion with a trap-fishery experiment (Worthington, 1950). This experiment is mainly a study of populations, but it has been necessary simultaneously to investigate the general biology of the perch, particularly the growth and related aspects. The computation of a formula to express the length-weight relationship and provide a means of interconverting measurements of length and weight revealed the relative complexity of the interrelationships of length, weight and condition. Condition in turn was found to be correlated with the seasonal changes in gonad development and growth, and the importance of the effect of stomach contents on weight had also to be assessed. It was decided, therefore, to combine these separate but interrelated aspects in one paper.

The main part of the paper is devoted to the questions of length-weight relationship and condition. A brief review of the fundamental bases for the concepts of length-weight relationship and condition and of some of the methods of analysis of length-weight data precedes an account of the application of the chosen methods to the present material and its results. This is followed by an account of seasonal changes in gonad weights. A brief account is then given of the rather scanty data available on the weight of stomach contents. The seasonal changes in condition are then described and, finally, some of the results are summarized, combined and discussed as a picture of the seasonal cycle in the Windermere perch.

In the statistical analysis of the length-weight relationship the data for only one group of fish are given in full (Tables 1 and 2) as an example of the method of computation used for all the groups. Again, in the section on seasonal changes in gonad weight and condition Figs. 2–7 are based partly on tables of data which are not published. The full tables have been deposited with the Freshwater Biological Association, from whom copies can be obtained.

2. THE ANALYSIS OF LENGTH-WEIGHT RELATIONSHIP AND CONDITION

Data on the lengths and weights of fish have commonly been analysed to yield biological information. One or other form of such analysis has, in fact, become one of the standard methods employed in fishery biology. Often, however, the examination of length-weight data has become so stereotyped that confused thinking on its aims, the methods employed and the results obtained has resulted. It is not proposed to enter here into a discussion of the

literature, but only to present an outline of the principal methods that can be used in the analysis of length-weight data before describing the application of some of these methods in the present work.

The analysis of length-weight data has usually been directed towards two rather different objects. First, towards describing mathematically the relationship between length and weight, primarily so that one may be converted into the other. Secondly, to measure the variation from the expected weight for length of individual fish or relevant groups of individuals as indications of fatness, general 'well-being', gonad development, etc. Throughout this discussion the term *length-weight relationship* is applied rigorously to the first category, while the term *condition* is applied as a rigorous but general term for length-weight analyses of the second category.

The length of a fish is often more rapidly and accurately measured than the weight. Moreover, back-calculations of past growth from scales, etc., usually yield data on length alone. Thus it is very convenient to be able to determine a weight where length only is known, and occasionally it may be useful to reverse this process. It has been found that the length-weight relationship of most fish can adequately be described by a formula of the type:

$$W = aL^n, \qquad (1)$$

where W = weight, L = length, a is a constant and n an exponent usually lying between 2·5 and 4·0 (Hile, 1936; Martin, 1949). For an ideal fish which maintains the same shape, $n = 3$, and this has occasionally been observed (Allen, 1938). In the vast majority of instances where length-weight relationships have been calculated, however, it has been found that the cube law is not obeyed and $n \neq 3$. Further, most species of fish do change their shape as they grow (e.g. Martin, 1949) and so a cube relationship between length and weight would hardly be expected. It is, therefore, more logical as a general basis for investigation to assume that probably $n \neq 3$. It has also been found that while n may be different for fish from different localities, of different sexes, or for larval, immature and mature fish (different 'growth stanzas') it is often constant for fish similar in these respects. The length-weight relationship may thus be a character for the differentiation of small taxonomic units, like any other morphometric relationship. It may also change with metamorphosis or the onset of maturity, as has been shown for other relative growth ratios (Frost, 1945; Huxley, 1932). Further, the exponent n is the ratio of the logarithmic growth-rates for length and weight, the increment in log weight for any period of time (of reasonable length) being n times the increment in log length for the same period of time. Thus the length-weight relationship formula (1), besides providing a means for calculating weight from length, and a direct way of converting logarithmic growth rates calculated on lengths into growth-rates for weight, may also give indications of taxonomic differences and events in the life history such as metamorphosis and the onset of maturity.

The length-weight relationship may be expressed graphically by plotting the observed lengths and weights as a dot diagram on double logarithmic graph paper. The points for fish having the same length-weight relationship will lie on a straight line with some scatter due to individual variation. This line represents the logarithmic form of equation (1)

$$\log W = \log a + n \log L, \qquad (2)$$

where n represents the slope of the line, and $\log a$ its position. Changes in the value of n can usually be readily observed as changes in slope. If the scatter is not too great, a line can be fitted by eye to each range in length having the points on a straight line, and its slope measured. It is usually possible in this way to judge the value of n to one decimal place, an accuracy adequate for a preliminary investigation. An accurate line can be computed from the same data by the regression method of least squares. Any one line should be fitted only to that range of size over which it is apparent that the fish have the same length-weight relationship. This range, and the accuracy of the fits, can usually be more easily judged by straight line graphs on logarithmic paper than by drawing curves on arithmetic paper. It is also important that the data from which the length-weight relationship is calculated should not have been subjected to any selection for weight against length. For example, gill-nets may select the fatter among short fish and the thinner among long fish, and thus lower the value for n, even though the means of length and weight may be unaffected (Kipling & Le Cren, unpublished data).

Individual variations from the general length-weight relationship have usually been considered more interesting than the length-weight relationship itself, and have been frequently studied under the general name of 'condition'. In some cases the specific gravity of the fish may not be unity, and variations in the specific gravity of the flesh of fish have been shown to occur (Tester, 1940) and their importance in studies on condition has been discussed by Kesteven (1947). Usually, however, in all but completely demersal fishes the density of the fish as a whole is maintained the same as that of the surrounding water by the swim bladder, and therefore changes in weight for length are due to changes in form or volume and not specific gravity.

Such changes in condition have usually been analysed by means of a *condition factor* (or 'coefficient of condition', 'ponderal index', etc. (Thompson, 1942; Hile, 1936). This is calculated as a ratio between the observed weight and that expected from the observed length. The basis of the expected weight is that for an ideal fish in whose length-weight relationship formula (1), $W = aL^n$, $n = 3$, and thus obeys the cube law. Various types of condition factor have been used, but in one of the original ones the condition was measured by the constant c (equivalent to a in (1)):

$$W = cL^3, \tag{3}$$

therefore

$$c = \frac{W}{L^3}. \tag{4}$$

As, however, c when so calculated is often an awkward decimal number, the average value of c found by trial from formula (3) was incorporated into the formula, and a new condition factor K found that would vary about unity

$$K = \frac{W}{cL^3}, \tag{5}$$

for example

$$K = \frac{W}{0{\cdot}000427L^3} \quad \text{(Menzies, 1920).} \tag{6}$$

The value of c depends partly on the units used for weighing and measuring the fish; in formula (6) these are pounds and inches. In instances where the original value of c chosen was found to have only limited application, and K was found to average about some value approximating to, but not exactly 1, c has been further altered to a convenient round number and often changed into its reciprocal

$$K = \frac{CW}{L^3}, \tag{7}$$

for example

$$K = \frac{100W}{L^3} \quad \text{(Hile, 1936)} \tag{8}$$

(where L is in centimetres and W in grams). In this formula, which is widely used, c has ceased to be equivalent to a in formula (1) and no attempt is made to make $K = 1$ on average. All these formulae are based on comparison with an ideal fish, whose $W \propto L^3$, and in subsequent discussion the term *condition factor* and its symbol K are applied only to measurements of condition so derived.

Differences in condition factor have been interpreted as measuring various biological features such as, fatness, suitability of environment or gonad development. The number of variables that can affect the value of K is however considerable, and some of them will now be briefly discussed. They fall into three main groups.

First, there are those factors correlated with length which affect the condition factor because the fish does not in fact obey the cube law in its length-weight relationship. The condition factor will vary with length itself according to the expression

$$K \propto L^{n-3}. \tag{9}$$

Thus length itself and any correlated factor will affect the values of K. This means that, except in the rare instances where $n = 3$, the condition factors of fish of different lengths cannot be directly attributed to features other than length. Further, factors such as age, sex or maturity which may affect the value of n, may in turn affect the values of K. Differences in mean K for fish from different environments may be due to the fish exhibiting racial differences in form, which will affect n and through it, K. Thus differences in K attributed to environmental factors may in fact be genotypic.

Secondly, the values of K may be affected by selection in sampling. The effect of gill-nets on the computation of length-weight relationships has already been mentioned, they may also be selective for condition factor (Farran, 1936; Deason & Hile, 1947).

Thirdly, there are those features usually associated with K. General, long-term, features such as environment, food supply and degree of parasitization may affect the fish's condition directly, or where K is correlated with length, via the growth-rate and average size. Seasonal changes have frequently been studied with the aid of condition factors, which have been shown to be correlated with gonad cycles, rate of feeding, etc. Short-term cycles of alternating growth in weight and growth in length have also been revealed by the use of condition factors (Brown, 1946).

In view of this list of widely different factors that can affect the condition factor, it is not surprising that the interpretation of K is difficult and often leads to erroneous results. As an example a hypothetical instance will be discussed. The population of a fish species is being studied for comparison in two lakes. It is only possible to fish each lake on one occasion, and gill-nets are used. Lake A is fished in June and most of the fish are caught in a gill-net of 2 in. mesh, and average 20 cm. in length. Lake B is fished in August and most of the fish, which average about 30 cm. are caught in a gill-net of 3 in. mesh. Condition factors are calculated for each fish (according to formula (5)) and averaged for each lake. For lake A, $K = 0{\cdot}95$, for lake B, $K = 1{\cdot}03$. It is then concluded that lake B is a more suitable environment for the particular species. Actually the higher average condition factor in lake B could just as easily be due to: (1) slight racial differences in shape between the fish of the two lakes, (2) the

greater mean length (due to growth-rate or mortality-rate), (3) the fact that in August the fish are in better condition after a summer of feeding than soon after spawning in June, and (4) selection by the gill-nets.

In this hypothetical case further information on morphometric measurements, average size, growth-rate, time of spawning, etc., might have ruled out many of the possible causes for the difference in K, but probably would not have made it possible to attribute this difference to any one cause. It is thus clear that in using the condition factor great care must be exercised to decide for exactly what purpose the information on condition is required, and whether the condition factor will yield this information and give results undisturbed by the effect of variables other than those being studied. Where other variables affecting K can be controlled or eliminated, or where a biological feature can be shown to be highly correlated directly with K, the use of the condition factor may be valuable. There are, however, alternative methods of analysing condition which may be more suitable.

It is relatively easy to eliminate the effect on K of length and correlated factors by calculating a 'condition factor' based not on the 'ideal' length-weight relationship

$$W = cL^3, \tag{3}$$

but on an empirical, calculated length-weight relationship

$$W = aL^n. \tag{1}$$

The 'condition factor', in this case called the *relative condition factor* and designated by K_n to distinguish it from the condition factor K based on the cube-law, is calculated from the formula

$$K_n = \frac{W}{aL^n}. \tag{10}$$

In practice the length-weight relationship would first be calculated as the logarithmic formula (2), and smoothed mean weights, $\hat{W}$, for each length-group computed from this log formula or read off an accurate graph. The relative condition factors would then be calculated from the formula

$$K_n = \frac{W}{\hat{W}}. \tag{11}$$

The difference between K_n and K is that the former is measuring the deviation of an individual from the average weight for length, while the latter is measuring the deviation from a hypothetical ideal fish. The choice of which condition factor to use must be based to some extent on which of these two comparisons is the more relevant. Hile (1936) argues that a condition factor calculated from an empirical formula (of type (1)) fails to measure any change in form associated with change in length. This is true, but the change in form or condition associated with length is succinctly and accurately described by the value of exponent n, and, as Hile points out, the relationship between condition as measured by K and length is given by the expression

$$K \propto L^{n-3}. \tag{9}$$

With the relative condition factor, therefore, it is possible to distinguish between and measure separately the influences on condition of length and other factors; whereas these are not readily separated when the ordinary condition factor is used.

For a more accurate analysis of condition, where the data are adequate, use may be made of the length-weight relationship formula itself. It has usually been considered that the empirical length-weight relationship formula of type (1) can provide little information on condition (Hile, 1936). Unless the value of n in equation (1) is identical for the groups of fish whose condition is being compared, the value of a in this equation gives no measure of their relative condition, and is not comparable to c in equation (4). Usually, as Hile (1936) points out, there is a negative correlation between the values of a and n. Where, however, it can be shown that n is the same for two groups of fish, the values of a obtained in separate length-weight relationship formulae calculated for each group will be a direct measure of their condition relative to each other.

If it is expected that a large group of fish, containing a number of smaller groups the condition of which latter it is desired to compare, is suspected of being homogeneous in its length-weight relationship (a logarithmic graph of the length-weight data showing for instance one straight, but rather broad line of dots) then a length-weight relationship formula (2) can be calculated for each subgroup. The values of n determined are tested for homogeneity, and if as was expected there is no significant difference between them, a pooled regression can be calculated for the whole group combined and the values of a adjusted for this pooled length-weight relationship. These adjusted values of a are accurate measures of the relative condition of the subgroups, and the significance of the differences between them can be subjected to accurate statistical test (e.g. Snedecor, 1946; Goulden, 1939; Mather, 1943).

The computational labour involved in such an analysis of covariance is fairly large, but it is probably not much greater than that needed to calculate by formulae (7) or (8) a K for each fish and then find the mean value of K for each subgroup. Further analysis, within the subgroups, can be carried out by means of the relative condition factor, calculated

from the pooled value of n and the value of a for each subgroup.

The use of both the relative condition factor and the analysis of covariance of the length-weight relationship as methods of directly comparing condition is confined to comparisons between fish which are homogeneous for n in their length-weight relationship formulae. Comparisons between fish which have different length-weight relationships will normally have little relevance. If they differ in size, differences between relative or ordinary condition factors will be difficult to interpret; if they are of the same length the weights themselves can be compared. Comparisons between such groups of fish can perhaps best be expressed by graphs of lines on logarithmic scales representing their respective length-weight relationships.

To sum up this review, it may be concluded that the expression of length-weight relationship and the measurement of changes in condition are two rather different but interconnected aims in the analysis of length-weight data. The length-weight relationship can best be expressed by a formula of the type $W = aL^n$ (1), and is most conveniently calculated and graphed in its logarithmic form (2). The condition factor K, where $K = cW/L^3$ (7) being based on the cube-law, which rarely holds, is affected by length as well as many other factors. This makes its interpretation difficult. The effect of length may be eliminated by using a relative condition factor based on an empirical length-weight relationship. The analysis of covariance in the log length-weight relationship may also be used for abundant data, where there is homogeneity of the exponent n in the length-weight relationship. In any analysis exact ideas as to the aims are required, and the method of analysis should be chosen so as to yield the maximum unequivocal biological information.

3. THE LENGTH-WEIGHT RELATIONSHIP

(*a*) *Sources of material and methods of collection*

The data used for length-weight analysis were obtained from fish collected primarily for other purposes. These fish were collected in the years 1943–8, and were all caught in the north basin of Windermere. They were collected mostly in traps (Worthington, 1950) and seines, but also by angling and a few of the very large fish were caught in gill-nets. These latter are the only gill-netted fish that have been included in the determinations of length-weight relationship, though some fish gill-netted in 1948 have been included in the seasonal samples used for determining relative condition factors. No samples likely to have been selected for weight relative to length have been included in the calculations of the regressions of weight on length.

Length was measured from the tip of the premaxilla to the tip of the longest caudal fin ray stretched out posteriorly. Length measurements were usually made to the millimetre below, but occasionally to the $\frac{1}{2}$ cm. below. Age was determined from the opercular bone or from the length frequency distribution for fish in their first two years (Le Cren, 1947). Age has been designated by the number of completed years of life, but with the birthday moved to 1 January. Thus a fish hatched in June 1945 will belong to the O group till 1 January 1946, then to the I group till 1 January 1947, and so on. The sex and state of gonad was determined by internal macroscopic examination, for all but running fish. This was usually easy for fish in their second year and older, though in early summer it was sometimes difficult to distinguish between immature and recovered spent fish.

As the weights of the perch varied from 1 mg. to 1450 g., several balances were used in an attempt to weigh each fish to approximately the same relative accuracy. The smallest fish were weighed in batches of ten or more on an analytical balance to the nearest milligram. It was found impossible to obtain a wet weight for these larval fish exactly comparable with the wet weight for larger fish, owing to the relatively large weight of any surface water, and the speed with which this water and then the fish themselves dried up. In practice surface water was removed with blotting-paper and the fish then weighed before they had time to dry up. Fish weighing between 0·2 and 10 g. were weighed on an ordinary chemical balance to 0·01 g.; fish between 10 and 200 g. were weighed on a 'Butchart' swinging arm balance to the nearest gram and for the largest fish a pan balance accurate to approximately 1 g. was used. In all cases the fish were weighed intact with gonads and stomachs, and damp with surface moisture, but wiped clean of any adhering dirt.

(*b*) *Analysis of data*

When a fairly large number of weighings from different sizes of fish and different seasons had been collected, they were divided into a series of groups according to age, sex and maturity of the fish; and the time of year, and were then plotted as a series of 'dot diagrams' on double logarithmic graph paper.

These graphs revealed that the fish could be divided up into a series of sex, age and maturity groups, in each of which the length-weight relationship could then be described by a formula of type

$$\log W = \log a + n \log L. \qquad (2)$$

Further, it seemed probable that the constant n in the formula differed from one age, sex and maturity

group to another, but that it was the same for fish of the same group caught at different times of the year. The constant a, however, varied with the season of capture.

It was then decided to analyse the data with accurate statistical methods and the fish were therefore classified first into groups according to age, sex, maturity, and then into subgroups according to the time of year. The list of groups and seasonal subgroups is as follows:

(1) Larvae	Early summer
(2) O and I	August, September, spring, July, August, September, October
(3) Female immature II	April, May, June, July, August
(4) Female immature III and older	April, May, June, late summer
(5) Female mature	Spring, April and May (ripe), spent, late June, July, August, September, autumn
(6) Male mature	Spring, April (ripe), spent, late June, July, August, September, autumn

For each of these subgroups a regression was calculated for the logarithm of weight on the logarithm of length, by the method of least squares. The lengths were grouped in 2 mm. groups for the smaller fish and 5 mm. groups for the larger, while the weights were grouped in equal-sized logarithmic groups, varying from 0·06 to 144 g. in size. Frequency distributions of lengths, and even more of weights, from fish tend to the Galton-MacAlister distribution rather than the normal, although the lengths are usually very near the normal. Thus the logarithms of the weights are approximately normally distributed.

When this series of regressions had been calculated, it was clear that in general the results agreed with the approximations obtained graphically. The data were then analysed further for covariance (Snedecor, 1946, pp. 318–29; Goulden, 1939, pp. 253–9; Mather, 1943, pp. 119–28). The regressions for each group of subgroups were tabulated with their sums of squares and regressions; and then the sums of squares were calculated for: (1) the 'pooled' regression within subgroups, (2) the means of subgroups, and (3) the total for the whole group. As an example of these calculations the skeleton data for the mature female group are shown in Table 1. The series of data obtained for each group by this analysis of covariance provided a set of statistical tests of significance.

From the residual sums of squares for each subgroup were calculated the standard error and 95% confidence limits for the regression coefficient for each subgroup. The 'pooled' or 'within subgroups' regression is the best estimate of the regression coefficient for the whole group, as unlike the 'total' regression (given in the last line of Table 1), it is not affected by the arbitrary differences in mean length between the fish in the different subgroups. The standard error of the 'within subgroups' regression coefficient was calculated from the residual sums of squares and used to calculate 95% confidence limits and in a 't' test of the significance of the difference of the regression coefficient from 3. The residual sums of squares for the 'within subgroups' regression were used in a test of the homogeneity of the subgroup regression coefficients. The regression for the means of the subgroups does not have much value in this instance as the mean lengths were affected by arbitrary factors. The residual sums of squares for the means regression has, however, been used as a test of the significance of the difference between the subgroup means, when they have been adjusted for the general regression. This test is therefore a test of the significance of subgroup differences in weight corresponding to the grand mean length, or in fact a test of seasonal variations in relative condition. Two further tests are possible relative to the means regression. One tests the significance of the difference between the pooled regression coefficient and the means regression coefficient, and the other tests the significance of the deviation of the subgroup means from their own regression. As the means of the subgroups are affected by arbitrary selection of the length of fish caught in the samples from different times of the year these tests have little meaning in this analysis of length-weight relationship. A summary of the tests of significance for the female fish is set out in Table 2, as an example of the tests carried out for each group. In each case Bartlett's test of homoscedasticity was also carried out to verify the validity of the 'F' tests.

When the analysis of covariance had been completed for each group, the values of the adjusted means for each subgroup were calculated. This gave for fish of the grand mean length the smoothed mean weight at each season of the year and was thus an accurate measure of seasonal change in relative condition. The significance of these differences between the adjusted means had already been tested as described above.

Further, accurate graphs were drawn on double logarithmic paper for each group of fish using the regression coefficient b for 'within subgroups' and the adjusted value of a for the subgroup with the maximum value of a. From these graphs smoothed mean weights ($\hat{W}$) could be read off for any length. In certain cases these smoothed mean weights were

Table 1. *Data for regressions of log weight (y) on log length (x) for mature females, showing method of computation and analysis of sums of squares* (s.s.) *and degrees of freedom*

Subgroup	s.s. x	s.s. y	s. products xy	Regression coefficient b	s.s. due to regression	Residual s.s.	Degrees of freedom
Spring	1·06099	12·62806	3·64674	3·43711	12·53425	0·09381	93
April–May	1·08443	13·40003	3·71861	3·42909	12·75145	0·64858	392
Spent	1·26846	15·39107	4·33807	3·41995	14·83598	0·55509	257
Late June	0·37000	4·31748	1·24122	3·35465	4·16386	0·15362	119
July	0·20429	2·43482	0·69505	3·40227	2·36475	0·07007	51
August	0·40923	4·67813	1·35927	3·32153	4·51486	0·16327	122
September	0·41593	4·66059	1·37450	3·30464	4·54223	0·11836	104
Autumn	2·87077	33·59050	9·74773	3·39553	33·09871	0·49179	358
					Total	2·29459	1496
Total within subgroups	7·68410	91·10068	26·12119	3·39938	88·79585	2·30483	1503
					Difference	0·01024	7
Total between means of subgroups	1·10438	9·46914	3·08322	2·79181	8·60776	0·86138	6
					Total	3·16621	1509
Total	8·78848	100·56982	29·20441	3·32303	97·04713	3·52269	1510
					Difference	0·35648	1

Table 2. *Analysis of variance for data in Table* 1

Source	Sums of squares	Degrees of freedom	Variance	F	P
Due to total regression	97·04713	1	97·04713	63,000	<0·01
Between regression coefficients within subgroups	0·01024	7	0·00147	0·95	>0·05
Difference between 'pooled within subgroups' and 'means' regressions	0·35648	1	0·35648	233	<0·01
Deviation of means from means regression	0·86138	6	0·14356	94	<0·01
Residual	2·29459	1496	0·00153	—	—
Total	100·56982	1511	—	—	—

used to calculate relative condition factors, (K_n) by formula (11). Mean relative condition factors were then calculated for small samples of fish caught at different dates especially in the 'spring' and 'autumn' when the adjusted mean weights for the subgroups for the whole season were inadequate to trace detailed changes in condition.

(c) *Results*

The results of the analysis of the length-weight data will be presented group by group followed by a summary of the combined data.

Larvae. The graphical plotting of the data revealed that the few points for weights of larval perch lay off the line taken by the young fish of between 3 and 14 cm. in length and formed a fairly distinct larval length-weight regression. A regression was therefore calculated for all the lengths and weights of fish from hatching till they were 3·0 cm. long. The regression formula found was

$$\log W = 0{\cdot}68969 + 3{\cdot}59163 \log L.$$

The length of newly hatched fry was found to average 6 mm., and although accurate weighing was very difficult, several batches gave an average weight of 1 mg. per fish. The regression calculated for the larvae, because of the difficulty of weighing and the bulk weighing of the fish is not based on data quite comparable to the regressions calculated for older fish. It will be seen, however, from Table 3 that the regression coefficient of 3·59163 for the larvae is significantly greater than that obtained for any other group, and is significantly different from 3·0.

O and I. Between the time they reached a length of 3·0 cm. at an age of about 2 months, till the end

of their second growing season, the perch seemed to form a homogeneous group with their weight varying with approximately the cube of the length. Regressions were calculated for O group fish in August and September, and I group fish in the spring, July, August, September and October. These regression coefficients varied from 2·59831 to 3·18333 though most of them were very near 3·0, and the differences between them were not significant. The pooled regression coefficient was 3·0117, and it was not larger than those for the three later months, but the test of homogeneity showed that this difference is not significant. Bartlett's test showed, however, that the II group females were heteroscedastic, there being a significant difference in the variance of the subgroups. The cause of this remains obscure, but it means that the tests of significance based on variance ratios may be erroneous. The 2-year-old females may include fish which will remain immature, and which thus may make the group

Table 3. *Summary of regressions of log weight on log length for each group of fish, and the combined total*

Group	No. of fish	Range in length (cm.)	Range in weight (g.)	Regression slope, *b*	Homogeneity of regression within group	*b* significantly different from 3	Significant difference between adjusted means
O and I	667	3·0–14·0	0·22–28	3·012	Yes	No	Yes
♀ immature II	462	9·5–15·5	7–40	3·195	Yes	Yes	Yes
♀ immature III and older	131	11·0–18·5	11–70	3·053	Yes	No	Yes
♀ mature	1512	11·5–43·5	11–1250	3·399	Yes	Yes	Yes
♂ mature	640	10·0–44·5	7–1450	3·281	No (due to August)	Yes	Yes
Total	3412	3·0–44·5	0·22–1450	3·165	No	Yes	Yes
Larvae	323	0·65–2·95	0·001–0·25	3·592	—	Yes	—
♂ immature	35	8·5–26·5	5–180	3·243	—	Yes	—

Table 4. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of O and I fish*

Subgroup	Average date	No. of fish	Adjusted mean weight	Percentage of maximum weight
O, Aug.	11 Aug.	85	3·536	97·1
O, Sept.	5 Sept.	91	3·642	100·0
I, Spring	18 Apr.	209	3·084	84·7
I, July	21 July	106	3·468	95·2
I, Aug.	11 Aug.	29	3·538	97·1
I, Sept.	11 Sept.	135	3·493	95·9
I, Oct.	26 Oct.	12	3·327	91·4
Total	—	667	3·379	92·8

significantly different from 3·0. The adjusted subgroup means differed significantly from each other, thus showing that there were significant seasonal changes in relative condition. The adjusted means and mean dates of collection for each subgroup are set out in Table 4.

Immature females. At first all immature female fish were grouped together, but the trial plotting indicated that most of the 2-year-old females probably had a distinct length-weight relationship from those that were older. The immature females were thus divided into two groups by their age.

The I+ and II+ females had a pooled regression coefficient of 3·19506. The regression coefficients for the subgroups April and May were considerably heterogeneous. The adjusted means were very significantly different from each other (Table 5). After August, when they began to develop their ovaries in preparation for their first spawning the next spring, the maturing II females were classed with the mature females.

Some older females were found to remain immature. Some of these may be fish which mature late, others may never mature. However, they were treated as a separate group. The pooled regression coefficient is 3·05292, and this is not significantly different from either 3·0 or the regression coefficient of 3·19506 obtained for 2-year-old immature females, but it is significantly different from that for mature females. There was no significant difference

between the subgroup regression coefficients, but the adjusted means varied significantly (Table 6).

Mature females. This was the largest group, and details of the analysis of its length-weight relationship have already been discussed as illustrating the method of analysis, and set out in Tables 1 and 2. The pooled regression coefficient was 3·39938; this is significantly different from 3·0 and from all the other groups. There was some difference between subgroup regression coefficients, they ranged from 3·30464 to 3·43711 but these differences were not significant. The whole group shows significant heteroscedasticity with Bartlett's test, but when the 'spent' subgroup is omitted the result loses its significance. The spent fish were rather variable owing to the inclusion of many fish that were part recovered and some only just spent. The adjusted mean weights show considerable and significant variation (Table 7).

Mature males. The pooled regression coefficient is 3·28063 which is significantly different from 3·0 and from the other groups except for the 2-year-old females. There was no great variation among the subgroup regression coefficients except for August which was 2·95847 and the spring which was 3·48383 but based on only ten fish. The whole series were significantly heterogeneous ($P<0·01$), but when August is omitted the remainder are homogeneous. The data for August consist of only a few samples over a very limited range and thus may be atypical. The heterogeneity has been ignored in the further analysis of the results. The significant variation among the adjusted mean weights is very similar to that found for mature females (Table 8).

Immature males. The lengths and weights were recorded for thirty-five immature male perch of 2 years old or older. They gave a regression coefficient of 3·24253 which is not significantly different from that for mature males.

(*d*) *Discussion and conclusions*

Kesteven (1947) discussed the possibility of using the analysis of covariance in the treatment of length-weight data from fish, but the present work was started before his paper was published. As no other use of the method so far appears to have been made, the present analysis functions to some extent as a trial of the method. It has revealed information which would not have been shown if ordinary condition factors or a single length-weight relationship regression had been used. It is clear from the results described above, that no single regression will adequately describe the length-weight relationship for the perch. The fact that the length-weight relationship coefficient n was considerably greater than the cube would also have complicated the analysis of seasonal changes in condition by means of the ordinary condition factor. It might have been possible to split up the groups still further and carry out a more detailed analysis of covariance, but it is probable that the data that were available would not have warranted the extra computational labour involved.

The length-weight regressions for the various age, sex and maturity groups are shown as lines on a logarithmic graph in Fig. 1, and the successive changes in slope will be noticed in this figure. The regression coefficient for the older immature females is very similar to, and not significantly different from, that for the young immature fish of both sexes. This suggests that the change from this relationship to that of the mature fish is correlated with maturation rather than age. The older immature females may retain the length-weight relationship of the young fish because their gonads have not matured.

A detailed comparison of the length-weight relationship of perch from different lakes is not possible as different authors have used different methods of measurement and analysis. Perch, on the whole, would appear however to have a length-weight coefficient greater than the cube, although this is not invariably the case (e.g. *P. flavescens* Mitchill in Lake Michigan (Hile & Jobes, 1942)). Alm (1946) discusses the condition of perch from different lakes, and although there appears to be quite a number of exceptions there is apparently a tendency for the faster growing populations of perch to have a higher average condition. The Windermere perch would seem to be intermediate in condition to the Swedish examples Alm quotes, but perhaps to have a higher value for the length-weight coefficient n.

4. THE SEASONAL CYCLE IN GONAD WEIGHT AND CONDITION

(*a*) *Gonad weight*

The total weight of the perch as recorded included the weight of the gonads. As these change in size with the season, and when ripe may constitute a considerable fraction of the total weight, records were made at different seasons of the gonad weights of small samples of fish. It was also hoped that these weights would provide evidence of the season cycle in gonad development.

The perch were opened ventrally and the single ovary or both testes dissected out, an operation that could usually be accomplished in a few seconds. The gonads were then weighed complete. At first a rough chemical balance was used, and the gonads were weighed to the nearest 0·1 g., later a more accurate chain type balance was used and weights were recorded to 0·01 g. For the largest fish the

Table 5. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of II immature females*

Subgroup	Average date	No. of fish	Adjusted mean weight	Percentage of maximum weight	Percentage of August weight
Apr.	23 Apr.	46	14·9	81·9	85·2
May	20 May	70	16·1	88·5	92·1
June	21 June	55	18·2	100·0	104·0
July	20 July	116	16·9	92·9	96·7
Aug.	11 Aug.	175	17·5	96·2	100·0
Total	—	462	16·9	92·9	96·7

Table 6. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of III and older immature females*

Subgroup	Average date	No. of fish	Adjusted mean weight	Percentage of maximum weight
Apr.	21 Apr.	36	25·4	86·1
May	18 May	50	26·0	88·1
June	21 June	24	29·2	99·0
Late summer	5 Sept.	21	29·5	100·0
Total	—	131	27·0	91·5

Table 7. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of mature females*

Subgroup	Average date	No. of fish	Adjusted mean weight	Percentage of maximum weight
Spring	21 Feb.	95	50·6	88·5
Apr. and May	21 Apr.	394	55·4	96·9
Spent	22 May	259	46·5	81·3
Late June	21 June	121	52·0	90·9
July	22 July	53	55·9	97·7
Aug.	8 Aug.	124	56·5	98·8
Sept.	14 Sept.	106	57·2	100·0
Autumn	25 Oct.	360	53·0	92·7
Total	—	1512	52·85	92·4

Table 8. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of mature males*

Subgroup	Average date	No. of fish	Adjusted mean weight	Percentage of maximum weight
Spring	5 Feb.	10	18·9	86·3
Apr.	22 Apr.	161	19·2	87·6
Spent	25 May	46	18·5	84·4
Late June	21 June	82	21·0	95·8
July	20 July	112	21·0	95·8
Aug.	12 Aug.	153	21·7	99·0
Sept.	8 Sept.	56	21·9	100·0
Autumn	23 Oct.	20	21·6	98·6
Total	—	640	20·6	94·0

gonads were weighed on a 'Butchart' balance to the nearest gram. In every case an accuracy of at least 5% was obtained. In the case of the smallest immature fish, however, an accurate dissection and weighing of the minute gonads was not attempted.

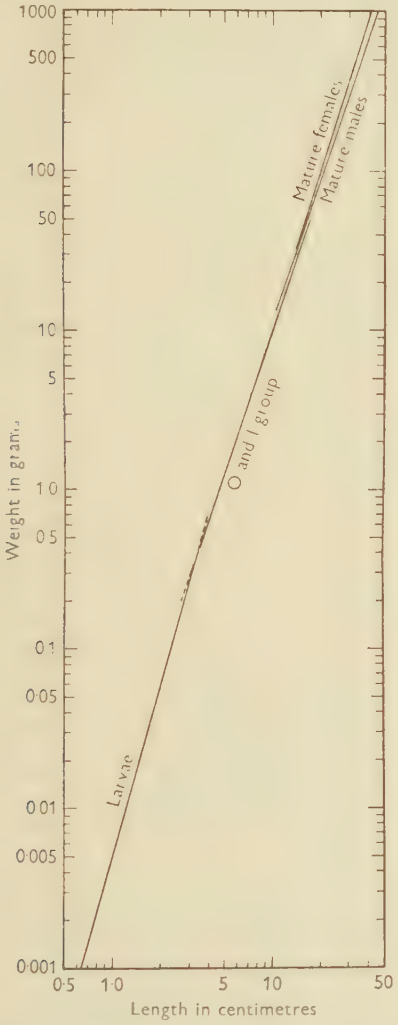


Fig. 1. The length-weight relationships of the perch. The regression lines for log weight on log length are given for *larvae, O and I group, mature females* and *mature males*. The regressions are those for the seasonal subgroups with the maximum relative condition.

First, for each fish whose gonads had been weighed a gonad:body-weight ratio was calculated and expressed as a percentage. It was then decided to determine whether this ratio altered with the size of the fish. Accordingly 'dot diagrams' were constructed of the logarithm of the gonad:body-weight ratio plotted against body weight. Graphs of this type were drawn for adequate samples of fish from different seasons. The data for mature females in February and October each gave a horizontal band of points on the graph. The points for very large fish weighing about 1 kg. also lay on the same horizontal band. The data for both ripe and spent fish in May in each case also showed no definite tendency for an increase or decrease in gonad:body-weight ratio with weight of fish. Data for other months, and for immature females, were less extensive and less conclusive. In the case of male fish, data for February, April, August and September were plotted, and in each case were not inconsistent with the conclusion that the gonad:body-weight ratio is constant at any one season for any size of fish. It can therefore be concluded, that although there is some individual variation in the gonad:body-weight ratio, it tends to be constant at any one season for all sizes of fish of the same sex and state of maturity.

Once it was clear that the gonad:body-weight ratio did not alter with size of fish, mean gonad:body-weight ratios of samples of fish that varied in size could be used to trace the seasonal changes in this ratio. The data for mature fish are plotted in Fig. 2. It will be seen that the ovary has a minimum size in mid-summer when it is quiescent. In August, however, it begins to increase in size, and this increase proceeds regularly through the winter and spring till the spawning time in May. At this time the gonad averages about 20% of the body weight. The freshly spent fish have empty ovaries weighing about 3% of the body weight. By the middle of June these ovaries have shrunk to about 1% of the body weight, at which ratio they remain till August. There is considerable variation among the different samples in the average gonad:body-weight ratio, especially in the spring, but this is almost certainly due to phenological differences from one season to the next. In 1947 in particular, after an unusually severe and late winter, the ratios in May were approximately equivalent to those for April in other years.

The mature male fish differ from the females in several ways. Development of the testes starts in August, but by October the testes have reached their maximum size, weighing about 8% of the body weight. They then remain this size through the autumn, winter and spring, till April. The average gonad weight then decreases through April and May till it is only 1–2% of the body weight. Quantitative data for the summer are nearly non-existent, but from visual observation it can be concluded that the testes remain small and quiescent through June, July and most of August. As the testes begin to be ripe early in April, the apparent fall in their weight from the beginning of April may

be due mainly to inevitable loss of milt with handling in capture and examination. These data on seasonal changes in the testes weight are very similar to those obtained for *Perca flavescens* Mitchill in America by Turner (1919), who also studied the histological changes in some detail.

The data for immature fish are very limited, but suggest that the gonad:body-weight ratio is relatively constant at about 0·5 % for immature females and does not change with size or season. This ratio ratio for all the forty-eight fish was 0·52 %. Individual ratios varied from 0·0 to 2·1 %; there did not seem to be any significant difference between the mean ratios for samples from June, August or September; or any correlation between the ratio and the size of the fish, though the data available are not really adequate to determine these features. The perch in Windermere are known to feed more heavily in summer than in winter (Allen, 1935), but even if they did not feed at all in winter, these

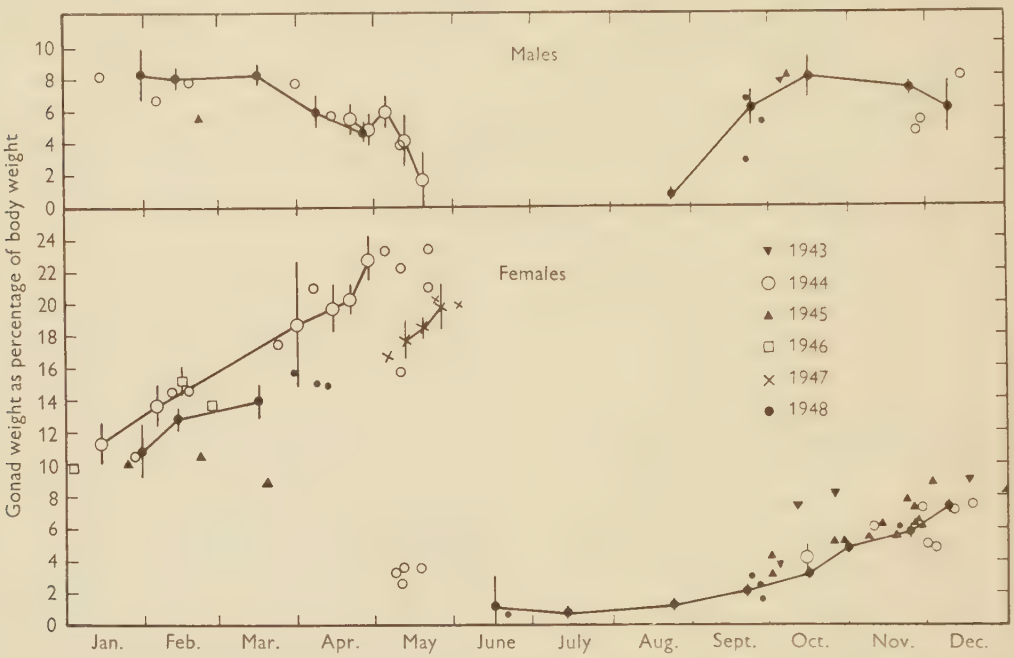


Fig. 2. Seasonal changes in the gonad weight as a percentage of the total body weight. The larger symbols are the means for samples of five or more fish with the vertical lines indicating 95 % confidence limits. The smaller symbols represent the means of samples of less than five fish.

of 0·5 % is approximately equivalent to that of the quiescent mid-summer ovaries of mature females. Although the evidence is not sufficient to be conclusive it suggests that this ratio begins to increase in normal females in their third August at the same time as the mature females begin to develop for spawning next spring, but remains constant throughout life in those females that still remain immature.

(*b*) *The weight of stomach contents*

In order to determine how much of the individual and seasonal variation in relative condition might be due to the weight of food in the stomach, the stomach contents of a few samples of perch seined in the summer of 1948 were weighed. The percentages of the total body weight contributed by the stomach contents were determined for each fish. The average stomach content:body-weight figures are adequate to show that, relative to the seasonal changes and individual variation in total weight, the weight of food in the stomach is not important. The weight of material in the remainder of the alimentary canal may nevertheless have some significant influence on the total weight, but visual observations suggest that the weight of the intestinal contents would tend to vary rather less than that of the stomach contents.

(*c*) *Condition*

The seasonal changes in relative condition are given in outline by the adjusted mean weights for the seasonal subgroup regressions for weight on length. These are presented in Tables 4–8. These data have been amplified by calculating relative condition factors for individual fish and finding the mean of these for each sample of fish from the two

years 1945 and 1948. These years were chosen to give a comparison between one year and another, and because they provided the most ample sources of data, but a few additional samples for the three spring and three autumn months from other years are also included. These means are plotted (with their 95 % confidence limits) in Figs. 3–7.

For the *O and I group fish* data from the adjusted mean weights of the regression only are available. It will be seen from Fig. 3 that the O group fish have a somewhat higher relative condition in September than the I group fish a year later. There is a considerable gap in the data between September and the following spring, but the low value of 84·7 % for the middle of April indicates that there must be a considerable fall in condition over the winter. A subsequent rise in the early summer is indicated by the higher values in July and August, but the detail of this increase cannot be followed without further material. As in the other groups the condition falls again in October, and presumably decreases throughout the autumn and winter.

In the case of the *II group immature females* the adjusted mean weight for June was thought to be unexpectedly high, and as it was based nearly entirely on one sample of fish, it was ignored, and the value for August taken as the basis (of 100 %) for calculating the relative condition factors. The points for the adjusted regression means in April and May and the sample means for that period, show that the relative condition is low at the beginning of April but then rises rapidly through May. The July adjusted regression mean may be aberrantly low, and the relative condition probably increases slowly through June, July and August. After August the II group immature females begin to develop their ovaries and join the mature female group.

Relative condition factors for the few females that remain immature though three or more years old are plotted in Fig. 5. Data are somewhat scanty, except for April and May, but it will be seen that these fish follow a similar pattern to the II group females. Condition probably falls slowly through January, February and March, but rises in May and June. In summer the maximum is probably reached early in September followed by a fall through the autumn.

For the *mature females* the data are more adequate and are shown in Fig. 6. The condition is fairly constant with perhaps a slight fall through January, February and March. In April it rises sharply, and at the beginning of May some samples of ripe fish have a mean relative condition factor of nearly 100 %. The ripe fish from later on in May, however, have much lower mean condition factors. Samples of newly spent fish have mean relative conditions of about 78–80 %. By 20 June the condition of the spent fish has increased considerably and this increase is continued through July, till by August the relative condition is about 99 % of the maximum in September. After the middle of September it falls sharply and by the middle of November it has reached an average value of about 91 %. It then continues to fall slowly through the winter and early spring.

The *mature males* present a picture similar to the mature females, except that the loss of relative condition on spawning is not so great (Fig. 7). There is evidence that the fall in condition from December to March is somewhat steeper than in the females. There appears to be a similar sharp rise in April followed by a general decrease through the latter part of April and most of May as the male fish spawn. This spawning process appears to take several days for an individual male fish, unlike the females who probably lay all their eggs in one spawning act. After spawning the males increase in condition rapidly and then more slowly throughout the summer to a maximum in September. The autumnal fall in condition does not begin until late in October.

(*d*) *Individual variations in relative condition and gonad weight*

The data on relative condition and gonad weight that have just been discussed have been based on mean values obtained for a number of fish. There is, however, considerable individual variation in both relative condition and percentage gonad weight. As a measure of this individual variation the coefficient of variation has been calculated for a few representative samples. For relative condition factors the values obtained varied between 6 and 17 %; while for ovary weight as a percentage of body weight the coefficient of variation ranged between 10 and 28 % and for testis weight from 8 to 36 %. The higher values were obtained at the spawning time or in the autumn when both the relative condition factor and the gonad weight were undergoing rapid change. As might be expected the greater individual variation shown at such times is probably due more to individual differences in the time of spawning or development of gonads than to inherent individual variations in condition or gonad weight maintained throughout the season, though the latter does occur to some extent. This greater variation at times of change is also shown by the greater range of the 95 % confidence limits for mean condition factors in April, May, June and October than at other times as illustrated in Figs. 4–7.

The individual relative condition factors for a number of large samples from August, September and October, the latter part of the growing season,

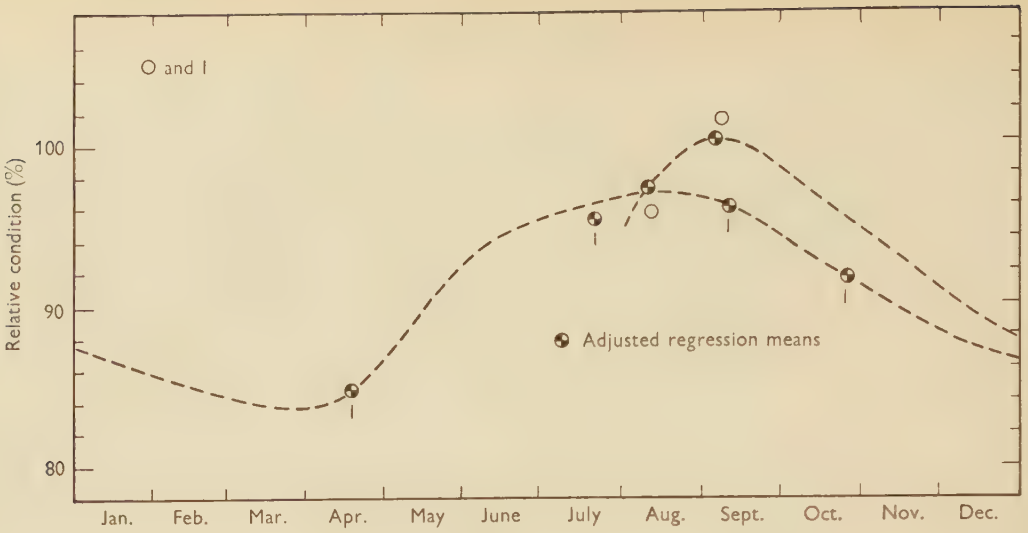
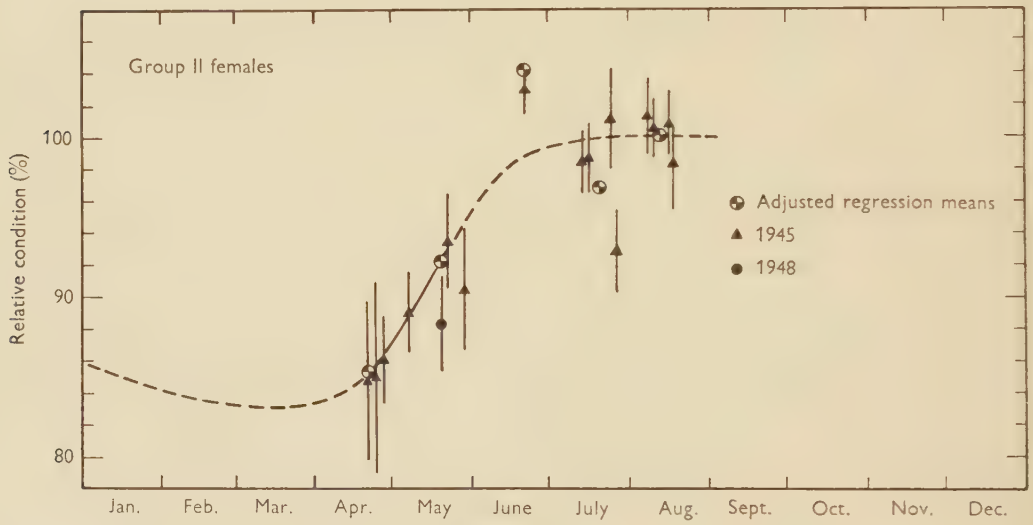


Fig. 3.



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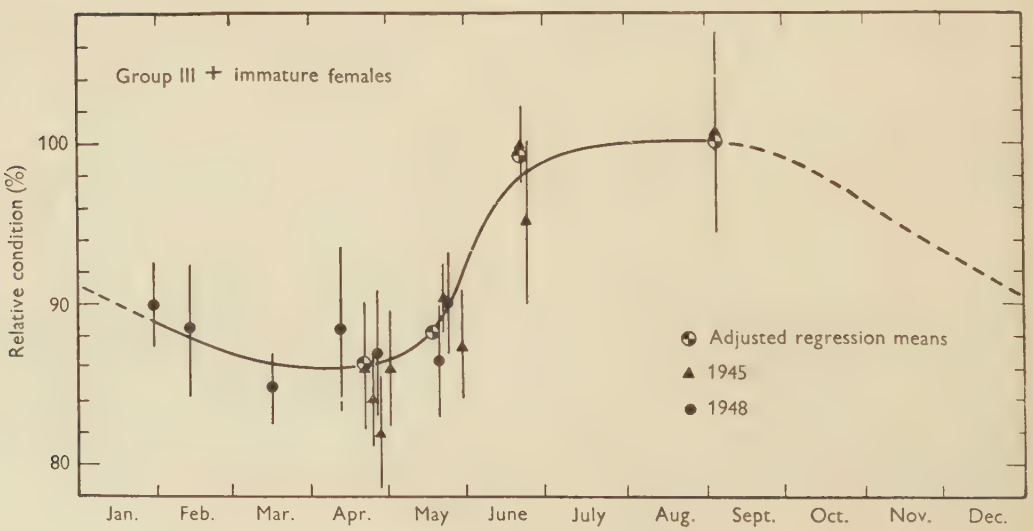

Fig. 5.

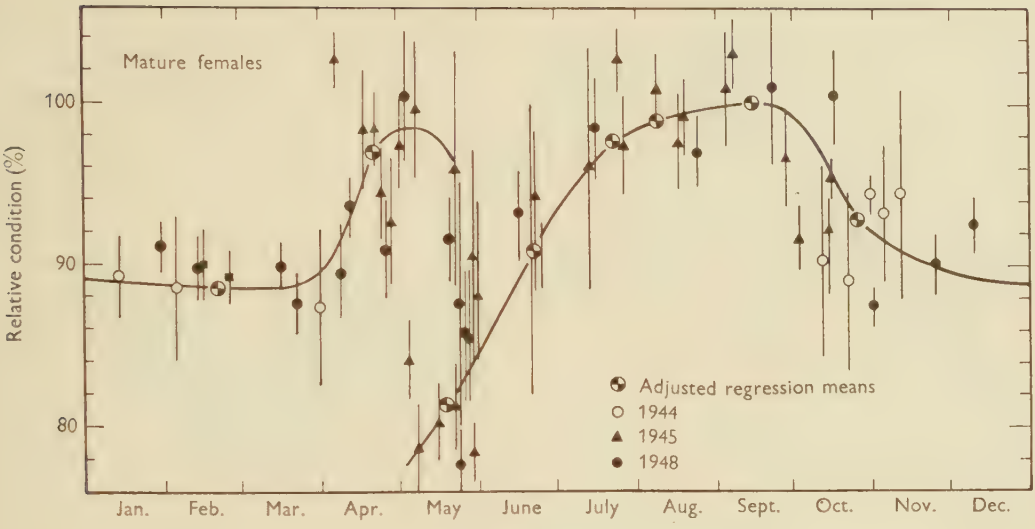

Fig. 6.

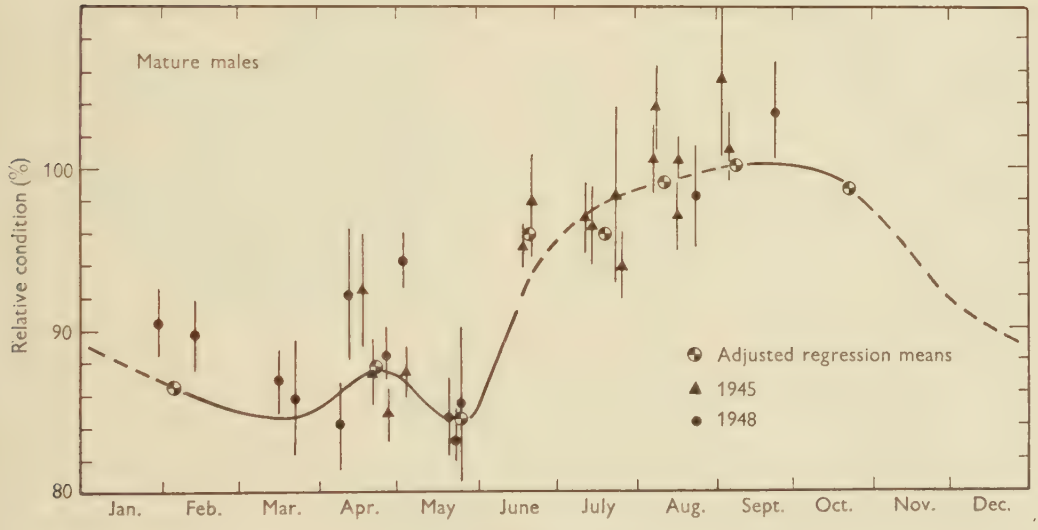

Fig. 7.

Figs. 3–7. Seasonal changes in relative condition expressed as a percentage of the maximum. The adjusted means for regression subgroups and the means of samples with their 95 % confidence limits are given. A curve has been drawn by eye through these points.

were also examined for correlation between condition and growth in length. It was suspected that those fish that were growing slowly in length as indicated by a small 'plus' growth for the current season, might also be growing slowly in weight and so be in poor condition. Further, those fish that were making the maximum increment in length might be doing so at the expense of weight and also be in poor condition. On examining the data, however, it was found that although one or two samples showed a very slight suggestion that such a correlation existed, the overall picture gave no indication that there was any correlation between growth increment in length and relative condition factor.

(*e*) *Discussion of the seasonal cycle*

It is to be expected that there will be a seasonal cycle in condition with a high level of condition during the late summer and a low level at the end of the winter. The immature fish (O and I group, II females, and III and older immature females) show this cycle with a minimum in March and April, a rapid increase in May and June, a maximum in August and September and a rapid fall in October and November.

These groups, and the mature males but not the mature females, also show a high value for condition in June and low in July, relative to the expected trend. This may be because most of the data for these 2 months comes from a few samples mainly collected in one year (1945) and may thus be aberrant. On the other hand, the younger fish were probably feeding mainly on zooplankton (Allen, 1935); and Smyly (unpublished data), studying the food and growth of O group perch in Windermere, has found that in some years there may be a shortage of littoral zooplankton about the middle of July. Thus the apparent July fall in condition might possibly be due to a temporary shortage of food for the smaller, plankton-feeding fish.

The effect of the actual weight of the gonads on the relative condition and its seasonal changes can be seen in Fig. 8, where the seasonal curve for condition is plotted with and without the percentage gonad weight subtracted. For convenience the lower curve may be termed the 'condition-minus-gonads', although it has been calculated indirectly from the data for average condition, and gonad weight as an average percentage of body weight, and not from calculating the condition of fish weighed after the removal of their gonads.

It will be seen from Fig. 8 that the curve for the mature females minus gonads is very similar to that for the immature females 3 years old and older, but that the seasonal fluctuation is rather greater. Again the curve for the mature males minus gonads is similar. It appears therefore that nearly all the difference between the seasonal curves for condition for mature and immature fish is due to the gonad-weight cycle in the former. For example, in the mature females the nearly constant level of condition through the winter, as contrasted with the continued fall in the condition of immature fish, is due to the increase in ovary size offsetting the fall in body weight. The rise in condition in April is further due to the continued increase in ovary weight concurrently with a slight increase in body weight.

This slight, and unexpected, rise in body-minus-gonad-weight in April before spawning has been examined in rather more detail by calculating condition-minus-gonads for a series of samples from 1944 and 1947. They confirm the suggestion from the general Fig. 8 that there is a slight rise in condition-minus-gonads in April followed by a slight fall, possibly due to the final increase in gonad weight just before spawning being made at the expense of body weight. A similar tendency is apparent in the males as well as the females. As, however, there is considerable individual variation it is doubtful how significant these relatively small changes are. It is impossible with the present data to elucidate them fully.

It appears then that the loss of weight on spawning is almost but perhaps not quite entirely due to loss of ova or milt and not general 'condition'. That some sacrifice in general body weight is made towards the build up of the ova is, however, indicated by the high rate of fall and subsequent low level of the condition-minus-gonads through the winter. It is significant that all the groups of fish, except the II group females, have their lowest level of condition-minus-gonads about the middle of April and the spring increase in condition starts at about the same time. In the II group females, however, it seems to start at about 3 weeks earlier.

In the mature males the development of the mass of the testes takes place in about 6 weeks between the middle of August and the middle of October. The curve for condition-minus-gonads of the males falls off steeply earlier than in the other groups, but the condition with gonads is maintained at a high level for longer into October than is the case for the females. Thus the development of both the testes and the ovary is made partly by maintaining a total body weight for length higher than normal and partly at the expense of the condition of the rest of the fish. It is significant that a large proportion of the food available for growth, and the growth potential of the mature fish, particularly the females, must be devoted each year to the annual production of gonad products.

It is hoped to provide some detailed evidence of the season when growth in length takes place in

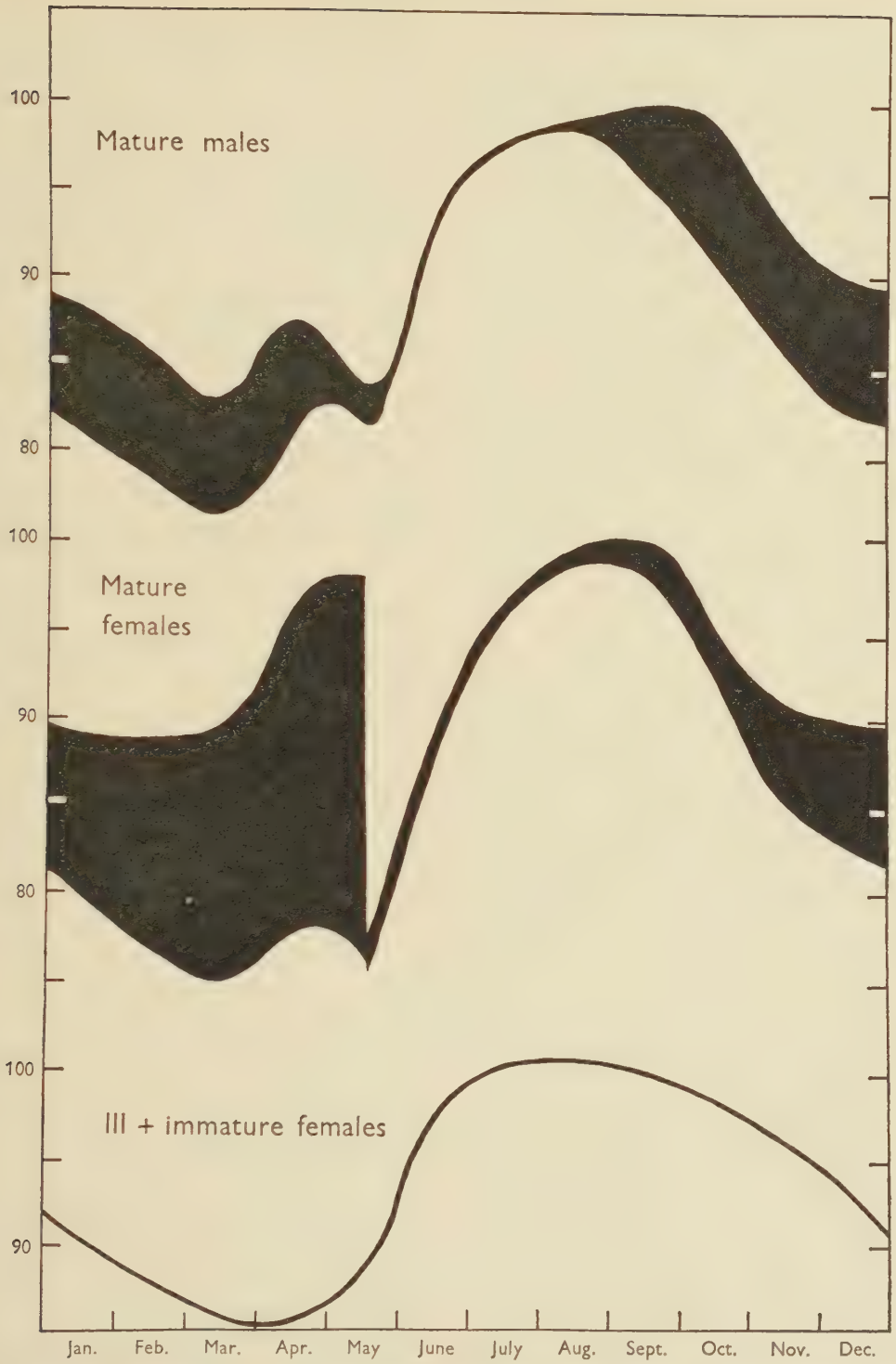

Fig. 8. Diagrammatic seasonal curves for relative condition with and without gonads. The solid black represents the gonad weight; the upper edge of the black the condition with gonads and the lower edge the condition-minus-gonads.

a later paper. It would seem, however, that the immature fish grow in length from early in May until early in October, but that growth is most rapid in June, July and August. The mature fish do not begin to grow in length until after the spawning season; probably about the middle of June and when the relative condition has reached 90–95 %. If the start of the growing season for length is correlated with some stage of the spring increase in condition, it would then be expected that the annual growth of immature fish, as compared with mature, might benefit from the longer growing season of the former. The females do grow more in their second year than the males, but the older immature females grow at about the same rate as mature females of the same age. These older immature females have in fact a spring increase in condition at about the same time as the mature females. It cannot be concluded however, from the evidence at present available, that the seasonal changes in condition are the sole factors controlling the growing season for length, although it would seem reasonable to suggest that a fish would recover the weight lost over the winter and in spawning before starting again to grow in length.

5. ACKNOWLEDGEMENTS

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6. SUMMARY

1. The methods of analysing length-weight data from fish are reviewed. Emphasis is laid on empirical formulae of the type $W = aL^n$, and the limitations of the conventional condition factor.

2. The length-weight relationship of perch of all sizes was determined from a series of regressions of log weight on log length, and an analysis of covariance. Relative condition factors were calculated for individual fish from smoothed mean weights obtained from the regression lines.

3. In length-weight relationship it was found that the perch could be divided into a series of six groups corresponding with age, sex and maturity. Each group was generally homogeneous within itself throughout the seasons, but usually differed significantly from the other groups. Relative condition was found to vary significantly with the season.

4. At any one season the gonad weight is a constant percentage of the body weight for fish of all sizes. The seasonal changes in gonad weight are described and differ somewhat for the two sexes. Stomach contents weigh up to 2 % of the body weight in summer.

5. There is a regular seasonal cycle in condition which is at its maximum in September and minimum in early spring. The different seasonal changes in condition between mature and immature fish can largely be accounted for by the cycle in gonad weight of the former.

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THE FLIGHT RANGE OF THE HONEY-BEE

By C. R. RIBBANDS

Bee Research Department, Rothamsted Experimental Station, Harpenden

INTRODUCTION

There are numerous records in beekeeping literature of honey-bees gathering honey from good crops growing 5 miles or more from their hives. Eckert (1933) even recorded colony gains from crops growing 7 miles away.

The usual flight range has been believed to be less than this, but most authorities have agreed that it is considerable. In Britain, Manley (1948) wrote that it covered '5 to 6,000 acres at least' and Wedmore (1932, p. 95) considered that 'the economical distance for honey-gathering is about 1 to 1½ miles'. N.A.A.S. Advisory Leaflet no. 344 (1949) stated that 'a locality that provides pollen and nectar continuously from early spring to autumn, within a radius of about 2 miles, is ideal for bees'. In the United States, Dadant (1946) suggested that apiaries might be placed 2–4 miles apart in hilly country, but that in open country they should be from 5 to 6 miles apart. Root (1947), however, stated that bees usually do not fly more than 1½ miles. He added that they would not go more than half a mile if they could obtain sufficient nectar within that distance, but that usually there was insufficient pasturage there.

The present experiments demonstrate that the economical distance for honey-gathering is sometimes not more than one-quarter of a mile; they emphasize the importance of weather in determining the flight range of the honey-bee.

METHOD

Crops on well-defined areas, as far as possible in isolation from other nectar-producing crops, were selected. Three apiary sites were then chosen for each experimental crop—one on the edge of the crop, one ⅜ mile from that edge and one ¾ mile from it (distances measured from 6 in. o.s. maps). The colonies of bees chosen for each experiment were first sited in one group upon some preliminary crop at least 5 miles away. They were weighed at the beginning and end of their sojourn there, and the gain or loss of each colony was calculated. These gains or losses were arranged in order of magnitude, and the colonies were divided into three subequal groups, in terms of these weights. One group was then placed at each of the experimental sites—0, ⅜ and ¾ mile from the crop. Each colony was again weighed at the end of the flowering period of the experimental crop, and its net gain or loss calculated. From these changes the average gain or loss of each group was deduced, and comparison of these averages provided the required experimental result.

In 1949 all the colonies were removed to one site on a post-experimental crop, and subsequent weighings determined the gains or losses of each group upon that crop. The results were then analysed statistically; these analyses were ultimately discarded as unnecessary, in view of the consistency and magnitude of the results.

Eight experiments were conducted. The first six were made upon three permanent crops—apple, lime and heather—in 1949 and 1950. The identical sites were used in successive years. Two additional experiments were made upon annual crops—cabbage and onion—in 1949. They could not have been exactly repeated.

The description just given is of the general plan, but some slight modifications were necessary. For the heather and onion experiments no suitable site was obtainable at ⅜ mile, so results at 0 and ¾ mile only are compared. In several experiments more bees were placed on the crop than at the distant sites, but the same attempt was made to produce a similar pre-experimental average for each group. In the second heather experiments an error vitiated this average, but this did not affect the final result.

THE EFFECT OF FORAGING DISTANCE UPON COLONY GAINS

The results from the apple crop are given in Table 1. The apples were grown in a modern cleanly cultivated 70-acre orchard. The bees at ⅜ mile could fly to this orchard, to a much smaller orchard or to a group of willows about the same distance away in another direction; with this exception the competing flora was sparse, most of the area being ploughed. In 1949 there was a substantial gain in colony weight both upon the crop and at ⅜ mile, but the gain at ¾ mile was less by 85%. In 1950 the small gain on the crop compared with a loss at ⅜ mile and a substantial loss at ¾ mile. In 1950, when the gain obtained was smaller, the absolute effect of distance was greater—a difference of nearly 15 lb. instead of one of 11 lb. between the colonies on the crop and those ¾ mile away.

The results from the lime crop are given in Table 2. The site was a double avenue of lime trees, 1 mile long. Bees were placed under the line of trees, and the alternative sites were measured at right angles to the avenue, from its centre. There were no isolated lime trees on the experimental side of the avenue but there was a considerable competing flora. In cooler weather this was mainly blackberry, which grew in fair quantity near the

Table 1. *Gain in weight of colonies at apple crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb. Before crop	During crop	After crop	Daily weather means
	1949:	11–22 Apr.	2–12 May	12 May–6 July	2–12 May
0	4	0	13·3 ± 2·7	46·5	sunshine 7·8 hr., max. temp. 58·1° F.
⅜	4	0·7	10·5 ± 2·6	40·3	
¾	4	− 0·9	2·0 ± 1·4	50·0	
	1949–50:	2 Nov.–2 Feb. (winter loss)	28 Apr.–18 May	18 Apr.–1 May	28 Apr.–18 May
0	8	− 16·5	3·0 ± 2·2	7·9	sunshine 4·9 hr., max. temp. 59·3° F.
⅜	4	− 16·2	− 4·4 ± 1·6	11·9	
¾	4	− 15·9	− 12·2 ± 1·1	6·9	

Table 2. *Gain in weight of colonies at lime crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb. Before crop	During crop		
	1949:	16–28 June	28 June–7 July	7–15 July	Total
0	3	13·50	15·6 ± 2·1	40·2 ± 4·6	55·9 ± 6·0
⅜	3	16·9	10·3 ± 2·3	43·7 ± 7·6	54·0 ± 9·5
¾	3	17·2	5·9 ± 1·6	26·5 ± 8·2	32·5 ± 4·2
	Daily weather means:				
	sunshine (hr.):		9·01	9·33	
	anemometer mileage:		85	77	
	max. temp. (° F.):		73·9	76·9	
	1950:	16–30 June	1–8 July	8–15 July	Total
0	4	1·9	9·9 ± 2·2	25·4 ± 4·2	35·3 ± 5·9
⅜	4	1·7	2·3 ± 1·2	22·1 ± 2·8	24·4 ± 3·4
¾	4	1·3	−0·1 ± 1·2	20·2 ± 3·8	20·1 ± 4·8
	Daily weather means:				
	sunshine (hr.):		2·95	9·25	
	anemometer mileage:		55	78	
	max. temp. (° F.):		64·2	70·1	

¾ mile site; there was an abundant supply of white clover throughout the experimental area, and on warmer days this was sometimes worked.

The results for both years are divided into two separate weeks. For each of the 4 weeks the bees at the crop gained more than those sited ¾ mile away, but the magnitude of this difference varied considerably. The combined results from both years showed that the gain at ¾ mile was 58% of that obtained at the crop, but during separate weeks this percentage varied from 1 to 79%. In both years the gains during the second week were substantially greater than those during the first week; although in both years the weather in the second week was better, this difference is mainly attributed to change in the state of the crop, which was at its peak of flowering during the second week. In the second week of 1950 the crop was greater and the effect of distance substantially less than in the first week of 1949. Weather conditions seem insufficient to account for this difference, which indicates that the effect of distance tends to be reduced when the quality of the crop improves.

The heather was dominant over the top of a Welsh moor, 1400 ft. high, and covered many hundreds of acres. The ¾ mile site was in the valley at 800 ft., and the bees there had to fly

uphill to their crop. In 1949 there was no competing flora, either in the valley or on the moor; in 1950 the valley held a good crop of white clover when the bees were transported there, and only the earliest heather flowers were then in bloom. Since it was thought that this might vitiate the experiment, all the colonies were weighed on 20 August when the white clover had finished, and the heather had just come into bloom. All colonies then showed losses, but those on the moor had lost least (5·5 lb. against 9·3 lb.), showing that no appreciable yield had been obtained from the white clover. In 1949, a superb heather season, the 15% difference between the two sets of colonies was not significant, but in 1950, a bad heather season, the final recorded gain ¾ mile from the crop was only 10% of the gain recorded at the crop.

The two experiments on annual crops were both conducted in 1949. They are recorded in Tables 4 and 5. The onions occupied a 15-acre field. There was some competition from clovers and hedgerow flowers, but none from other cultivated crops. The cabbages occupied an 8-acre field, with no competing crops. It had been intended to leave the bees here for a long period, but the severe losses led to quick removal to a more desirable site, to avoid possible starvation.

For the cabbage experiment colonies of widely varying size were used. Upon the crop the stronger colonies gained a little weight while the weaker ones lost slightly (individual change on cabbage, +0·8, +0·5, +0·4, −1·1, −2·75 lb., followed by gains of 14·9, 17·9, 23·6, 5·6 and 1·25 lb. respectively, upon the subsequent crop). Away from the crop the stronger colonies lost most (individual losses at ⅜ and ¾ mile from cabbage, 5·0, 4·6, 3·6, 2·9 and 2·3 lb., followed by gains of 29·5, 26·6, 10·9, 16·5 and 6·7 lb. respectively, upon the subsequent crop).

The results demonstrate that increases in foraging distance were consistently associated with decreases in colony gains; the magnitude of this effect was, however, very variable. At one extreme (Table 1, 1950) a distance of ⅜ mile eliminated any nectar gains, while at the other (Table 3, 1949) the colony gain was reduced by only 15% at ¾ mile.

A comparison of the total unweighted colony gains from all five crops in 1949 shows that the colonies at the crops gained 166¼ lb., while those

Table 3. *Gain in weight of colonies at heather crop*

Miles from crop	No. of colonies	Mean gain of colonies in lb. Before crop	During crop	Daily weather means
	1949:	15 July–4 Aug.	4 Aug.–20 Sept.	
0	7	34·6	59·6 ± 5·8	sunshine 5·9 hr., anemometer mileage 190, max. temp. 64° F.
¾	3	37·3	51·2 ± 2·1	
	1950:	1–15 July	4 Aug.–20 Sept.	
0	8	22·1	25·6 ± 1·2	sunshine 4·6 hr., anemometer mileage 379, max. temp. 60° F.
¾	4	30·3	2·45 ± 0·7	

Table 4. *Gain in weight of colonies at onion crop*, 1949

Miles from crop	No. of colonies	Mean gain in lb. Before crops 12 May–6 July	During crop 7–30 July	Daily weather means
0	4	50·9	38·0 ± 5·7	sunshine 7·5 hr., max. temp. 76·0° F.
¾	4	51·8	30·4 ± 7·5	

Table 5. *Gain in weight of colonies at cabbage crop*, 1949

Miles from crop	No. of colonies	Mean gain in lb. Before crop 10 Mar.–14 Apr.	During crop 28 Apr.–5 May	After crop 5–23 May	Daily weather means
0	5	−5·2	−0·4 ± 0·6	12·7	sunshine 6·6 hr., max. temp. 57° F.
⅜	2	−5·2	−4·8 ± 0·01	28·0	
¾	3	−5·4	−2·9 ± 0·3	11·4	

¾ mile from the crops gained only 113¼ lb.—a reduction of 32%. In 1950, a poor honey year, the colonies at the three crops gained 65·6 lb., while those ¾ mile from the crops gained only 11·8 lb.—a reduction of 82%. The breeding rate of a colony partly depends upon the quantity of incoming forage (Nolan, 1925), so that improved early gains produce an increased population of bees for subsequent foraging; these calculations make no allowance for any cumulative effect of distance which could thus be produced.

THE RELATION BETWEEN COLONY GAINS AND INCOMING PROVENDER

Consideration of the causes of the effects of distance should be preceded by an interpretation of the extent to which the data are related to the actual quantities of forage which were brought into the hive. Every day each colony consumed, for its sustenance, a considerable quantity of both honey and pollen. The quantity of food so dissipated depended both upon the number of bees and the quantity of brood in each colony, and probably ranged between ½ and 1½ lb. per colony per day. The duration of most of the experiments was so short that this loss was similar in each group of colonies, irrespective of their distance from their crop. Therefore an equal addition to all the colony net gains will provide an estimate of the proportion of forage brought in at each distance.

This factor helps to explain the sensitivity of colony net gains to weather factors, the magnitude of the distance effect, and the variation in that magnitude. For instance, if it is supposed that the cost of colony sustenance averaged 1 lb. per day during the first week of the 1950 lime crop, when the colony net gains varied with distance from 9·9 to −0·1 lb., the amount of forage carried into the hive (ignoring surplus water) would then only have ranged from 16·9 to 7·1 lb. Thus the colony net gain might have been eliminated by a 42% reduction in incoming provender.

Increases in incoming forage are at most slightly reflected in increased requirements for sustenance; they will therefore reduce the magnitude of the distance effect upon colony net gains. With the fullest possible allowance for this relation there is still a wide variation, not thus accounted for, in the magnitude of the distance effect, and this provides the clue to its main cause, a factor which is itself variable—the weather.

THE ROLE OF WEATHER IN PRODUCING THE EFFECT OF FORAGING DISTANCE

To obtain information concerning the effects of weather during the 1950 lime experiment, daily records were kept. One colony at each distance was weighed each evening at sunset. These records were compared with the daily weather statistics from Rothamsted Experimental Station, 4 miles away, and also with the gains from a colony at Rothamsted, close to another avenue of limes (Table 6). The record of the latter colony is not directly comparable with that of the others, because the weights were taken (for another experiment) at 9.30 a.m. each morning.

As expected, water-loss by evaporation from nectar during the night subsequent to a heavy crop substantially affected the daily evening weighings (10 July); in addition, there was evidence that substantial loss might also occur on at least the second night (comparison of colonies 8 July, when the poor performance of the at-crop colony could be attributed to water losses from gains of 5–6 July; size of losses on 11 and 16 July). Such continued water-loss makes it difficult to correlate daily changes in weather conditions with those in colony gains. A feature of the daily record is the considerable effect upon the total gain of a few outstandingly good days. After allowing for the subsequent loss of water the honey yield obtained on 9 July must have been a substantial percentage of the total yield. The effect of distance varies considerably from day to day. On 9 and 13 July it was not visible, but on 5, 6, 12 and 15 July it was substantial. In all the latter instances the effect can be attributed to unfavourable weather, but the major role was played by different weather components on different days.

The records from the colony in Harpenden have been included because they are believed to illustrate another aspect of the effect of distance. The main experiment was in a country district, not flooded with bees, but the Harpenden colony was sited on the edge of a residential area overpopulated with bees. This difference could explain how on the two best flying days (9 and 13 July) there were increased gains in the country colonies but not in the Harpenden colony; in the latter the better weather was counterbalanced by more intense competition from bees sited farther from the crop.

It was not possible to obtain daily records of colony gains during other experiments, because no portable automatic weight-recording apparatus was available. However, when the total colony gains in the various experiments are compared with the average weather conditions then experienced much of the variation of the magnitude of the distance effects seems explicable. The considerable effect of distance during the first week of the 1950 lime flow is associated with low temperature and sunshine records, and the difference between the two heather experiments with less sunshine, lower temperature

Table 6. *Comparison of daily colony gains during lime crop, with weather records from Rothamsted* ($3\frac{1}{2}$ *miles south*)

	July 1950														
	1–4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Sunshine (hr.)	—	**0·0**	**0·8**	6·1	9·1	**12·1**	7·0	6·5	8·4	**9·3**	12·2	**1·8**	10·3	4·6	**2·2**
Maximum temperature (° F.)	—	**62**	**65**	71	75	**81**	67	66	68	70	68	66	67	65	69
Rain, hours (including following night)	—	0	3·3	0	0	3·5	4·0	0·4	0·6	3·3	0	9·0	0·1	0·4	0
Anemometer mileage	—	41	21	26	29	40	111	101	**137**	**36**	93	84	82	119	**120**
Weather generally	—	Bad	Bad	—	—	Good	—	—	Bad	Good	—	Bad	—	—	Bad
Gain in lb.															
Colony at crop	6·25	6·6	3·25	0·25	1·0	9·55	−1·0	1·75	7·4	4·1	1·0	3·5	−4·6	1·05	2·1
Colony at $\frac{3}{8}$ mile	−5·25	2·1	1·6	2·5	4·5	14·5	−5·0	−0·4	3·6	8·2	−0·1	0·75	−1·75	−1·0	1·0
Colony at $\frac{3}{4}$ mile	−3·25	1·9	1·9	2·5	3·25	9·25	−3·6	−0·75	3·6	6·75	1·0	0	−2·6	−0·4	0·6
Colony in Harpenden	0·05	2·6	2·3	2·25	4·45	3·2	−1·25	0·55	1·45	2·0	2·05		−2·7	−0·1	−1·05

Table 7. *Calculated effect of foraging distance upon nectar intake*

Minutes for complete trip, including unloading; hive on crop		5	15	30	60	120	240
Percentage reduction in nectar intake	At $\frac{3}{8}$ mile	39	18	10	5	3	1
	At $\frac{3}{4}$ mile	56	30	18	10	5	3

Table 8. *Five-minute counts of returning bees, near sunset*

G.M.T.	Distance from crop on 12 July			Distance from crop on 14 July		
	0	$\frac{3}{8}$ mile	$\frac{3}{4}$ mile	0	$\frac{3}{8}$ mile	$\frac{3}{4}$ mile
8.30	666	512	272	1110	952	279
8.45	372	118	14	244	122	48
9.00	112	15	2	19	0	2
9.15	80	0	0	0	0	0

and more wind during 1950; a small distance effect during the onion experiment is associated with warm weather, and a considerable effect during the cabbage experiment with cold weather.

THE ROLE OF FLYING TIME IN THE EFFECT OF FORAGING DISTANCE

Causes other than weather may contribute to the distance effect; the most obvious of these is the time and energy wasted by bees in flying the required distance. The energy consumed is negligible (Beutler, 1950), but the time may be appreciable. Since bees fly at about 14 m.p.h. (Park, 1923) it will take them about $3\frac{3}{14}$ min. for a return trip of $\frac{3}{8}$ mile; it is easy to calculate the effect of this increased foraging time upon nectar intake (Table 7).

To obtain an estimate of the likely magnitude of this cause, a large number of bees working from a hive at the 1950 lime crop were individually marked, and on 12–13 July, in favourable flying weather (see Table 9), a continuous watch was kept on the hive entrance and the times of incoming marked bees were recorded. Thirty-two records were obtained. Since the longest and the shortest times were likely to be least reliable, since they might include bees missed during an intermediate return, or bees returning without a full load, the upper and lower eight records were discarded. In the remaining half the mean time for the complete trip (including unloading) was $40{\cdot}3 \pm 5{\cdot}9$ min.

With such a foraging time, and when the magnifying effect of colony sustenance on net gains is allowed for, the effect of distance upon colony gain might have been completely accounted for, in some experiments, without postulating any other influence.

OTHER EXPERIMENTAL FACTORS

A minor factor is the effect of distance upon colony flight near sunset (20.13 G.M.T.). This was investigated by making simultaneous counts of the numbers of returning bees, for 5 min. periods, at 15 min. intervals, at a hive at each distance from the 1950 lime crop (Table 8). These observations showed that flighting continued later at the colonies nearer to the crop. It is not unlikely that flighting from such colonies also commenced earlier in the morning.

Sometimes during heavy honey-flows new comb foundation had to be added to the colonies. In all such cases allowance was made for only the exact added weight, but the necessity for drawing new comb must have been a disadvantage. The colonies which gained most drew out most new comb, so this factor could only have tended to minimize the distance effect, and may be ignored.

Throughout the experiments every effort was made to keep all the colonies in a non-swarming condition. However, for the 1950 lime experiment owing to the bad weather in June it was found necessary to include, in each group, one colony which had just commenced to rear queen cells. These cells were cut out both at the commencement of the lime flow and at weekly intervals thereafter. Each colony with cells was the poorest member of its group; in the preliminary period the three cell-producing colonies had averaged 0·9 lb. more than the others, but during the fortnight of the lime experiment their mean net gain was $13{\cdot}3 \pm 3{\cdot}8$ lb., while the others gained $32{\cdot}7 \pm 3{\cdot}6$ lb. This happened in spite of the reduced breeding rates of the cell-raising colonies. It illustrates a practical consequence of Taranov's (1947) observation that swarm bees tend to cluster in the hive, and do not reinforce the foragers.

DISCUSSION

The present results must be compared with those obtained in the United States by Eckert (1933), and by Sturtevant & Farrar (1935). Eckert's work was done in Wyoming, where for three seasons he placed groups of colonies in an arid region, devoid of crops, at various distances at half-mile intervals from an irrigated area. Colonies within 2 miles of the irrigated area gained equally with those upon it. Sturtevant & Farrar compared a group of 30 colonies sited 1 mile within an irrigated area with a similar group sited $1\frac{1}{2}$ miles from the edge of the area ($2\frac{1}{2}$ miles from the first group). In 1931 the average gain of the distant colonies was 59 % of the average gain (73 lb.) of those among the crops; 1932 was a better year, and between 22 June and 16 August (after making allowances in respect of stolen supers) the distant colonies gained 91 % of the average gain (218 lb.) of the others. Sturtevant and Farrar (1935, p. 589) concluded that 'apiaries located out some distance from the nectar source may not always do as well as those surrounded by a considerable area of nectar-secreting plants', but 'if necessity requires the placing of apiaries appreciable distances away from the nectar source..., other things being equal, the beekeeper can secure a quite satisfactory honey crop'.

Such conclusions could not be derived from the present results. The explanation may lie in the different conditions of the American experiments, for they took place in a dry district where flying conditions were probably uniformly favourable, and the bees were sited in an area, but not upon a crop. The most valuable crops may have been at a distance from all the colonies, thereby reducing the differences between the relative mileages covered

by the various groups. Lunder & Lunder (1946), working upon the heather crop in Norway, obtained a 37% decrease in yield when bees had to fly more than $1\frac{1}{4}$ miles to the crop—a result not inconsistent with my 1949 experience with heather.

The results emphasize that the optimum foraging range is much less than the maximum one. They illustrate the importance of weather in determining foraging range. The effect of flying time is proportional to the speed at which the crop is gathered; it is therefore most considerable in respect of pollen crops, which often take only a few minutes to collect (Ribbands, 1949). The relation of these results to problems of practical beekeeping will be discussed elsewhere (Ribbands, 1951).

ACKNOWLEDGEMENTS

I am pleased to acknowledge the helpfulness of the farmers who provided the apiary sites for these experiments, and the help given throughout the experiments by members of the Bee Department at Rothamsted. In particular, the heather experiments could not have been conducted without the willing assistance of Messrs M. Hassanein and J. S. Simpson.

SUMMARY

The gains in weight of groups of colonies of honeybees sited on the edge of crops were compared with those of groups sited $\frac{3}{8}$ and $\frac{3}{4}$ mile away from the same crops. Experiments were repeated in two successive years, under different weather conditions.

Increased flying distance was consistently detrimental, but the magnitude of the effect varied considerably; the reductions in the gains ranged from 15% at $\frac{3}{4}$ mile to 100% at $\frac{3}{8}$ mile. In 1949 the reduction in total gains at $\frac{3}{4}$ mile from five nectar crops, was 32%; in 1950, from three crops, the reduction was 82%. Reduced colony gains of up to 25%, at $\frac{3}{4}$ mile from the crop, could be attributed to increased flying time. The greater reductions were associated with unfavourable weather. Distance also reduced colony flighting near sunset.

The effect of distance upon colony net gains is much greater than its effect upon the quantity of forage brought into the hive; an instance is cited in which colony gain could have been eliminated by a 42% reduction in incoming provender.

Colonies in a pre-swarming condition gained much less than 'balanced' ones.

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OBSERVATIONS ON THE ORIENTATION OF SOME SPECIES OF BARNACLES*

By H. BARNES, D. J. CRISP† and H. T. POWELL

The Marine Station, Millport and I.C.I. (Paints Division), Marine Biological Station, Brixham

(With Plate 6 and 9 Figures in the Text)

INTRODUCTION

There are in the literature a number of conflicting statements regarding the effect of various stimuli on the cypris stage of barnacle larvae, before and at the time of metamorphosis, and little experimental work has been done to elucidate the type of reactions involved. Visscher (1928), working with *Balanus amphitrite*, *B. improvisus* and *Chthamalus fragilis*, stated that during the earlier part of their free-swimming stage the cypris larvae were positively phototropic, but later the reaction to light became erratic, and at the time of attachment was decidedly negatively phototropic. He further stated that in a settlement experiment they orientated with the anterior end (i.e. with the paired eyes) away from the light source. However, MacDougall (1943) working with two of the above species (*Balanus improvisus* and *Chthamalus fragilis*) and also *Balanus eburneus*, and Pyefinch (1948) working with *B. balanoides* and *B. crenatus*, both state that the cypris larvae retain their positive reaction to light up to the time of settlement.

There also appears to be some disagreement regarding the orientation at, and subsequent to, metamorphosis of several species of barnacles. Moore (1935), in considering *B. balanoides*, has suggested that if a barnacle is settling in a current, then at the time of settlement it is likely to be orientated with the current. A general orientation at right angles to the current was supposed to be due to rotation after settlement. This rotation was considered to be a response to the orientation of the beating cirri in relation to the current; it was suggested that feeding would be more effective with the animal orientated across the current. Alternatively, Moore suggested that a vertical orientation might be due to elimination by competition (on the above feeding hypothesis) of those barnacles not settled across the current. These observations are not in agreement with the work of Hiro (1939) and MacDougall (1943) who found that the settled cyprids of *B. amphitrite*, *B. improvisus*, *Chthamalus fragilis* and three species of *Tetraclita* were orientated even in a current with the eye spots towards the source of light, so that subsequently the barnacle lay with the carino-rostral axis vertical and the cirri beating downwards. MacDougall found that this orientation was absent in cyprids settling during the night, and experimental work strengthened his suggestion that light was the factor responsible. Both Hiro and MacDougall suggest that the discrepancy between their observations and Moore's explanation may be due to the higher current speeds at Moore's site (maximum 2 knots in contrast to 1 knot at their site). However, this explanation seems inadequate, since Smith (1946) has shown that settlement of certain Balanids only takes place at low current speeds, e.g. maximum speeds of 0·8–1·0 knot for settlement of *Balanus eburneus*, and 1·0–1·3 knots for *B. improvisus*.

That orientation with the carino-rostral axis in a given direction is present in many cirripedes has then been clearly shown; the present work demonstrates this in the following species: *B. balanoides*, *B. crenatus*, *B. improvisus*, *B. perforatus*, *B. amphitrite* and *Elminius modestus*. Sometimes this orientation is so strong as to be readily observable; in other cases it can only be demonstrated by careful measurement and analysis.

MATERIAL AND METHODS

The detailed observations concern *Balanus crenatus*, *B. balanoides* and *Elminius modestus*. With the first two species large panels (15 × 10 in.) and small glass slides (3 × 1 in.) exposed in a vertical position from a raft have been used; the method of exposure and details of the site at Millport have already been described (Pyefinch, 1948). In analysing these

* This work was carried out independently at Burnham-on-Crouch and West Mersea (Essex) on the one hand (D.J.C.), and at Millport on the other (H.B. and H.T.P.). As the results obtained were clearly of a similar nature and led to the same general conclusions, it was thought desirable to present and discuss the evidence in a joint publication.

† Now at the Marine Station, University College of North Wales, Bangor.

results relatively large areas were counted and the orientation rarely fell outside $0° \pm 90°$ (see below); it could therefore be readily demonstrated by frequency-orientation-angle histograms. In the work on *E. modestus* small panels were used and exposed at inter-tidal levels in the estuaries of the Rivers Blackwater and Crouch, Essex.

With some of the *E. modestus* material the orientations were most conveniently treated as vector quantities. The orientation (ϕ) of each of a small number (up to 30) of randomly chosen individuals was measured to the nearest 10°. The direction was resolved vertically (A) and horizontally (B) and the summed components $\Sigma_i (\cos \phi_i)/N$ and $\Sigma_i (\sin \phi_i)/N$ calculated; where ϕ_i is the angle to the vertical of the ith individual, and N is the total number of individuals in the sample; A and B are the mean vertical and horizontal components respectively. ϕ is taken as 0° vertically upwards, $\pm 180°$ downwards, with positive values in the clockwise direction. Now $\tan \theta = B/A$ and the resultant $R = \sqrt{(A^2 + B^2)}$. For a randomly orientated population, A, B and R approximate to zero, while θ may have any value according to the chance direction of sampling errors. If orientation is real, θ will differ significantly from zero and R will offer a measure of both the strength and, in conjunction with the sample number, the significance of the value of θ. For complete orientation $R = 1{\cdot}0$.

In all subsequent descriptions and analyses the orientation will be referred to the carino-rostral axis, and the eye spots in the cyprid before metamorphosis will be regarded as anterior; thus a barnacle which is vertically orientated towards daylight will have the carino-rostral axis vertical (0°) and the cirri beating downwards.

THE ORIENTATION OF THE BARNACLES

Orientation relations of the young and older stages

If Moore's (1935) suggestion were substantiated that rotation takes place after settlement and metamorphosis, it would affect all considerations regarding orientation and its cause; this question will therefore be considered first. Most of the detailed observations regarding this problem refer to *Balanus crenatus*, with a smaller number of observations on *B. balanoides* and several other species. Six ground glass slides (3 × 1 in.) exposed during the spring settlement of 1950 and having about ten newly settled barnacles per slide, were brought into the laboratory and divided into two equivalent sets. Each set was fastened by rubber bands on to a vertical sheet of glass, and the latter suspended in separate tanks through which passed a gentle flow of sea water. Each set was illuminated by means of a 25 W. electric lamp 25 cm. away from the tank, the illumination being in one case from above and in the other from below, the remaining sides of the tanks being blacked out. The initial orientation of each barnacle was marked on the ground glass slides with a pencil mark. Observations were made at frequent intervals over a period of 9 days, throughout which the barnacles remained quite active. The barnacles were all very young, newly metamorphosed *B. crenatus* from 0·84 to 1·0 mm. in length and were in general orientated with this long axis vertical; they had settled with the anterior end of the cyprid towards the light as described by MacDougall (1943).

In neither set was there any change in orientation during the experiment, suggesting that if light were the factor responsible for the original orientation, it is effective only at attachment or during the initial stages of metamorphosis, and that there is no further response immediately subsequent to metamorphosis, that is in the stages figured by Runnström (1925) in his figures 9–12. It should be noted that, although the barnacles remained quite active and some growth and development took place during the experimental period, the growth was less than that of comparable young barnacles growing under more natural conditions on similar slides suspended from the raft. However, at the same time the orientation of a number of young *B. crenatus* (0·80–1·17 mm. in length) was similarly noted on slides kept throughout on the raft. The dominant initial orientation was again vertical. These latter barnacles have now been under observation for 12 months, and neither during the early growth stages nor subsequently has any change in orientation taken place. In addition, one slide of marked barnacles was inverted on the carrier and replaced on the raft. No change in the orientation of this original settlement took place, although the later spat was again orientated vertically, with the carinal end uppermost, so that the cirri were beating in the opposite direction to those of the inverted barnacles of the original settlement. Further, during the course of a year's observations on the growth-rate of several hundred barnacles (*B. crenatus* and *B. balanoides*) settled on ground glass slides, no evidence of any rotation whatever has been noted. The results clearly indicate that whatever may be the factor responsible for orientation, it is effective for *B. crenatus* and *B. balanoides* only at settlement or during the very earliest stages of metamorphosis.

This statement is equally true for *Elminius modestus*. Thus Fig. 1 shows a well-defined orientation of *E. modestus* cyprids; the panel was 30 × 10 cm., painted with a non-toxic composition and exposed in a vertical position at M.L.W.N. at West Mersea,

from 17 May to 14 June 1946. The orientation of adults on the same panel is also shown. It is evident that the primary orientation is due to the direction of attachment of the cyprids and that no change in the mean orientation of the population accompanies metamorphosis. (In recently metamorphosed individuals the paired eyes are often very clearly marked and are situated at the rostral end of the carino-rostral axis owing to the inversion of the body at metamorphosis; see also p. 239). Another set of observations is given in Table 1 (see also p. 236). It will be noted that the mean orientation shows no significant change between size groups from the cypris stage of individuals of 2 mm. or so in length. Photographic records of panels which had been rotated through 90 and 180° have shown that with this species also no detectable change in orientation occurs among settled individuals of a size greater than 1 mm., although in subsequent settlements the barnacles were again orientated in accordance with the changed position of the panel.

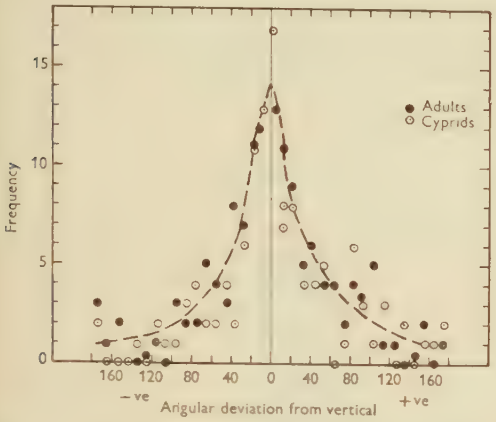


Fig. 1. Orientation of adults and cyprids of *Elminius modestus* on the same panel, exposed intertidally.

Growth-rate and orientation

The above observations are not in agreement with Moore's suggestion (1933, 1935) that rotation occurs during the growth of *Balanus improvisus* and *B. balanoides*. His alternative explanation for *B. balanoides* was that there is a relation between feeding efficiency and orientation so that those barnacles orientated horizontally (i.e. along the current) are eliminated by competition. A large number of individual barnacles (*B. crenatus* and *B. balanoides*) has been measured at intervals over a period of 12 months: measurements of carino-rostral length, width and height were made, but for the present paper the carino-rostral length is considered to be an adequate measure of growth. All the individuals were growing without restriction on raft-exposed slides, from which all other settling organisms were cleaned at each inspection. Since (see later) most of the barnacles settled with their carino-rostral axis vertical, individuals with this axis horizontal are few. Fig. 2 shows the relation between the mean angle (grouped in 20° sets) and the mean specific growth-rate for each group for three consecutive periods. It is clear that, within this range of orientation angle, there is no significant difference of growth-rate.

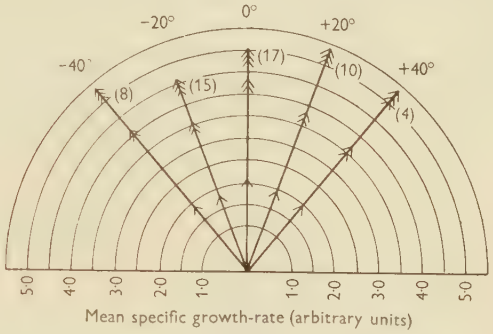


Fig. 2. The relation between mean angle and mean specific growth-rate for three consecutive periods of growth of adult *Balanus crenatus*. Growth-rate is indicated by length of line to each successive arrow. Figures in brackets indicate number of barnacles in each set.

Table 1. *Orientation and size of cyprids and adults of* Elminius modestus

Size group ...	Cyprids–0·9 mm.	1·0–1·4 mm.	1·5–1·9 mm.	2·0–2·4 mm.
Number in sample	53	66	30	16
Mean square angular deviation from means*	46·1°	39·6°	30·0°	42·7°
Mean direction	−8·5°	−7·0°	−5·7°	−6·2°

* $\Sigma(\theta-\bar{\theta})^2/(n-1)$, where $\bar{\theta}$ is the mean angle of a sample of n individuals.

An analysis of variance of the results is given in Table 2 and, since one is not here concerned with the changes of growth-rate, the data refer (as in Fig. 2) to separate growth periods usually of about 18 days, the mean age being shown in the table. The degrees of freedom in each series are the same for all the periods. Three sets of results are given, two for *B. crenatus* and one for *B. balanoides*.

A comparison of the mean squares clearly indicates that orientation has no significant effect on the growth-rate for any of the periods investigated. The absence of horizontally orientated barnacles, i.e. -70 to $-90°$ and $+70$ to $+90°$ is to be noted. However, in series II there was one *B. crenatus* at $+78°$, and in the *B. balanoides* series one at $-90°$. The specific growth-rates for the several periods of these two individuals, together with the mean specific growth-rates and the standard deviation for all the comparable barnacles, are given in Table 3. It is clear that these horizontal barnacles are also not significantly different in their growth-rate and can be regarded as drawn from the same population.

Further, panels which had been rotated through 90 or 180° (*Eliminius modestus*) did not show any significant difference in population mortality compared with controls.

Table 2. *Analysis of variance of growth-rate of* Balanus crenatus *and* B. balanoides *in relation to orientation angle, for four and three consecutive periods respectively; orientation angles grouped in 20° sets*

(*a*) *Balanus crenatus*; Series I (16 individuals)

(Five orientation angle groups of 20° from $-50°$ to $+50°$.)

Source of variation	Degrees of freedom	Mean square ($\times 10^6$) Period 1, 14 days	Period 2, 27 days	Period 3, 47 days	Period 4, 65 days
Between angle group means	4	104	105	18	18·3
Between individuals of group	49	109	57	11	11·8

(*b*) *B. crenatus*; Series II (17 individuals)

(Five orientation angle groups of 20° from $-50°$ to 50°.)

Source of variation	Degrees of freedom	Mean square ($\times 10^6$) Period 1, 12 days	Period 2, 27 days	Period 3, 54 days
Between angle group means	4	103	147	29
Between individuals of groups	24	76	144	31

(*c*) *B. balanoides*; (17 individuals)

(Four orientation angle groups of 20° from $-50°$ to $+30°$.)

Source of variation	Degrees of freedom	Mean square ($\times 10^6$) Period 1, 12 days	Period 2, 27 days	Period 3, 54 days
Between angle group means	3	89	31	27
Between individuals of group	16	101	149	34

Table 3. *Mean specific growth-rate of* Balanus crenatus *and* B. balanoides *over orientation range* $-50°$ *to* $+50°$, *compared with two individuals outside this angular range*

	Period 1	Period 2	Period 3
		B. crenatus	
Mean specific growth-rate	0·062	0·038	0·020
Standard deviation	0·009	0·012	0·006
Individual at $+78°$	0·063	0·067	0·020
		B. balanoides	
Mean specific growth-rate	0·051	0·045	0·022
Standard deviation	0·010	0·011	0·006
Individual at $-90°$	0·062	0·040	0·020

The orientation of adults

The orientation of fully developed *Balanus crenatus* may be illustrated by reference to two series of observations. In the first of these the orientation angle ($0 \pm 90°$) was measured of 103 barnacles growing without restriction, on a smooth

bakelite panel, exposed during the late summer of 1949. Fig. 3 gives the frequency of barnacles for each 20° angle and clearly shows the dominant orientation with the carino-rostral axis towards the vertical, although the distribution is slightly skewed.

In a similar manner the angles of 231 barnacles which had been under observation for some months during 1950 were measured after 4 months' growth, and the frequency distribution per 20° angle is shown for this set in Fig. 4; this confirms the previous results.

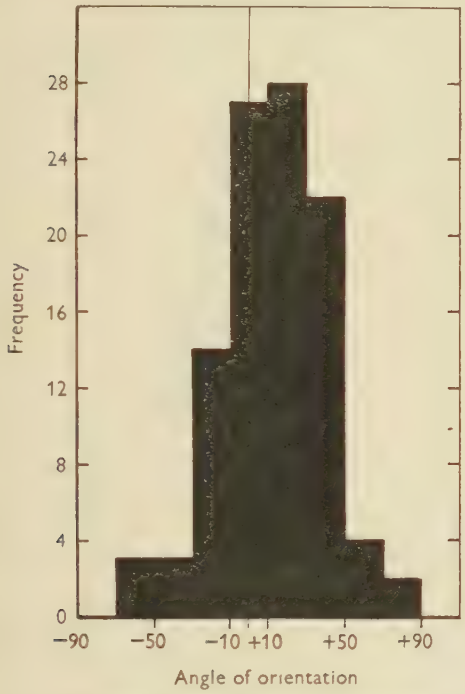


Fig. 3. Histogram of frequency-orientation-angle (20° groups) of adult *Balanus crenatus*, on a bakelite panel (15 × 10 in.) exposed from raft during late summer 1949.

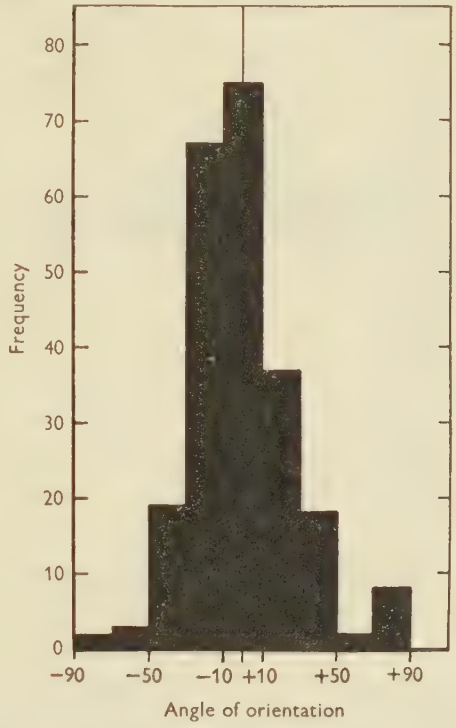


Fig. 4. Histogram of frequency-orientation-angle (20° groups) of adult *Balanus crenatus*, on ground glass slides exposed from raft during spring and early summer 1950.

The orientation of 100 cyprids of both *B. balanoides* and *B. crenatus* taken at random from a single panel exposed during 1950 is shown in Fig. 5, which again confirms the previous results.

Orientation towards the vertical is also shown in intertidal settlements of *B. balanoides* provided the light is mainly falling from above. Fig. 6 shows the orientation of *B. balanoides* on a vertical panel painted with non-toxic composition exposed at M.L.W.N. on a wooden pontoon facing south between 30 April and 2 July 1946 at Neyland, Pembrokeshire. The reverse side was almost entirely obscured from the light and received only a sparse settlement, chiefly at the lower edge which received light from below; here the orientation was reversed, the cirri beating upwards.

It is necessary to demonstrate that this orientation is reproducible in a series of similar situations at any one time, and in the same situation at different times, so that the possibility that it is a contagious phenomenon due, for example, to the influence of the current produced by the cirral beat of one individual on the orientation of a later settler adjacent to it, may be eliminated. If this were the case there appears to be no reason why the initial settlement should always display the same orientation. This has been clearly demonstrated in a series of experiments on *Elminius modestus* at Burnham-on-Crouch. Twenty-two panels (4 × 3 in.) were mounted on a wooden frame in two rows, each being inset to a depth of 0·5 in. and being thereby isolated from its neighbours; each panel was thus as nearly as possible under identical conditions (see Pl. 6, phot. 1).

The reproducibility of orientation in *E. modestus* may be illustrated by the following results. Four kinds of panel (plain glass, half ground glass with the ground part uppermost, half ground glass with

the plain part uppermost, and bakelite) were mounted, as described above, and exposed facing south at mean low-water level at Burnham-on-Crouch, on 4 September 1947. Observations were made and photographs taken on 12 and 19 September 1947, and after the end of the autumn settlement. During this whole period settlement was relatively light, so that complications due to crowding were avoided, and mortality of newly metamorphosed barnacles was very low (<5%). The figures set

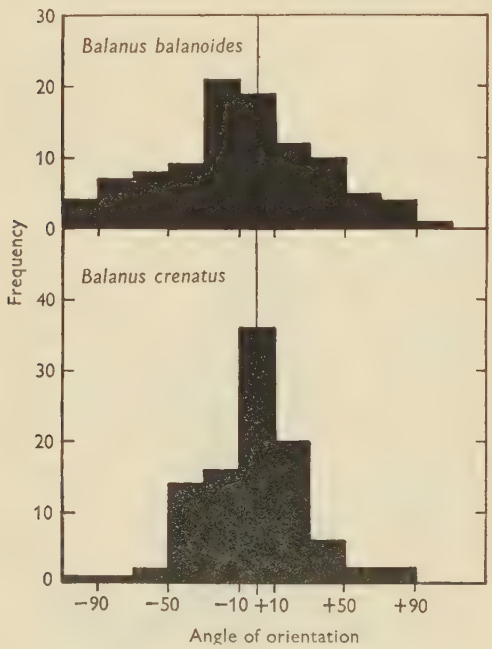


Fig. 5. Histogram of frequency-orientation-angle (20° groups) of cyprids of *Balanus crenatus* and *B. balanoides*, on the same bakelite panel (15 × 10 in.) exposed during spring 1950.

out in Table 4 show that although the number of cyprids was variable between the different cells, the general direction of their orientation was always with the scuto-tergal axis pointing upwards, and moreover, the majority settled on the upper part of the panels. In order to show that the orientation effect is independent both of the season of settlement and of the density or rate of settlement, Table 5 has been set out. This gives the orientations and resultants for the positions I–II, together with the dates of exposure and densities of the final settlement. The orientations are of the same order as in Table 4.

Several other points of interest emerge from this series. For example, Table 4 does not indicate two other positional features which are quite striking: first, that the orientations are not simply upwards but also inwards from the sides of the panel (see Pl. 6, phot. 2, a typical case); and secondly, that the greatest settlement is usually in the middle of the panel approximately three-quarter way up from the base and coincides with a 'neutral region' where orientation is almost or quite random. This is roughly where the shading effect of the upper wall of the cell would counter-balance the illumination falling from above. Further, it is also clear that the positional effects above are much more important than variation in the character of the surface of the panel in determining the distribution of settlement between and within the cells. The number of *E. modestus* settling does not bear any clear relation

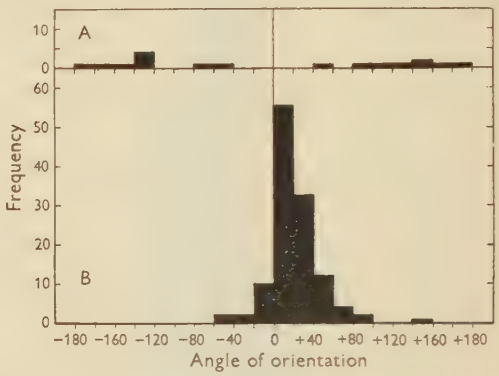


Fig. 6. Histogram of frequency-orientation-angle (20° groups) of intertidal *Balanus balanoides* at Neyland, Pembrokeshire. A, back of panel, light from below; B, front of panel, light from above.

to the type of surface, differing in this respect from *Balanus balanoides* which does not settle so readily on plain, or even ground glass, as on roughened bakelite.

It should be noted that panels 6 and 10 (Table 5) refer to settlements of *B. balanoides* in which the same orientation is apparent; panel 10 was reversed and re-exposed to *Elminius modestus* settlement shortly afterwards with a resulting reversed orientation (−180°) as shown.

The relation of orientation to light

The orientation described above, with the anterior end of the cypris larva facing upwards, might conceivably be due to the influence of gravity, particularly if settlement in the intertidal experiments on a receding tide left the cyprids hanging vertically downwards attached by the antennules. It is equally possible that light is the orientating factor, and this will be shown to be the case. With the *Balanus crenatus* and *B. balanoides* results from the raft, orientation to the vertical is quite clear, and the skewness, apart from sampling errors,

Table 4. *Settlement and orientation of* Elminius modestus *on vertical panels in identical cells facing south and unobstructed*

(A, bakelite with sand-papered surface; B, half frosted glass, with upper half frosted; C, as B but with lower half frosted; D, plain glass.)

Position	Type	Settlement 4–11 Sept.	Settlement 4–19 Sept.	Settlement 4 Sept.–10 Oct.	Percentage on upper half	Orientation (θ)	Resultant (R)
1	A	11	65	91	52	− 2°	0·61
2	B	7	25	61	6·2	+12°	0·37
3	D	3	16	58	81	+18°	0·48
4	C*	0	3	9	89	+ 6·5°	0·91
(5	B	0	1	1	—)	—	—
6	C*	2	8	20	65	+11·5°	0·57
7	B	6	28	64	92	+11·0°	0·84
8	C*	0	1	10	80	+24·5°	0·42
9	B*	3	5	15	80	−28°	0·13
10	D	12	70	122	76	0°	0·70
11	A	8	65	124	77	− 9°	0·60
12	A	2	30	42	88	+ 1°	0·64
13	C*	0	4	20	95	+25·5°	0·53
14	D	11	110	205	77	−32·5°	0·53
15	B	1	19	67	90	−32°	0·20
16	C*	1	6	34	97	−29·5°	0·16
17	A	3	12	39	92	−17°	0·19
18	D	3	42	139	88	−10·5°	0·35
19	D	10	100	205	79	− 7°	0·47
20	B	4	62	120	89	−37·5°	0·77
21	C	4	12	43	81	+19°	0·54
22	A	10	32	133	90	+29°	0·82
Means							
0–11					75·4	+ 6·3°	0·55
12–22					87·8	− 2·5°	0·40

* Fewer than 30 individuals available.

Table 5. *Orientation data for* Elminius modestus (*and* Balanus balanoides *at positions* 6 *and* 10 *only*) *settled at different times of the year, and at different densities and rates of settlement*

Position	Type	Date exposed	Date withdrawn	No. per sq.cm.	Percentage on upper half	Orientation (θ)	Resultant (R)
1	B	7 Sept. 1948	24 Apr. 1949	1·8	7	+16°	0·63
2	C	7 June 1948	6 July 1948	19	52	+ 2°	0·69
3	B	6 July 1948	3 Aug. 1948	22	54	− 4°	0·74
4	B	27 Apr. 1948	9 June 1949	35	49	+ 1°	0·62
5	A	12 May 1949	9 June 1949	37	50	+ 3°	0·80
6	A	21 Oct. 1948	12 May 1949	1·0	91	+18°	0·67
7	A	3 Aug. 1948	7 Sept. 1948	7·0	67	− 8·5°	0·69
8	B	7 Sept. 1948	21 Oct. 1948	10	43	− 5°	0·84
9	D	7 June 1948	6 July 1948	17	56	+19°	0·81
10	A	13 Feb. 1948	11 May 1948	2·1	51	− 1°	0·65
11	A	12 May 1949	4 Sept. 1949	9·5	52	+18·5°	0·75
22	A	27 Apr. 1948	7 Sept. 1948	36	48	+ 7·5°	0·90
Mean					52	+ 4°	0·72
10^1	A	11 May 1948	7 June 1948	12	43	−180°	0·38

10^1, reversed and re-exposed to *E. modestus* settlement.

could readily be explained on the hypothesis that there was shading caused by the beams of the raft. Some detailed results on the settlement of *Elminius modestus* will now be given in support of the light-orientation hypothesis.

A frame of panels similar to that already described was erected at M.T.L. at Burnham-on-Crouch during July 1948 beneath a wooden jetty with overhanging sides, facing east across the direction of the tideway. The position was such that the upper row of eleven cells received light slightly from below, while the lower row received light slightly from above through the gap between the river-bed and the overhang of the jetty, as indicated by arrows in Fig. 7. The orientations and positions of the settlement are shown in Table 6: the orientations are clearly in the direction of the source of illumination, while the distribution of the settlement is also influenced by the same factor. The settlements on the upper row to which the incident light came mainly from below and from the sides are concentrated in the lower half of the panel and orientated downwards, while those on the lower row, illuminated from above, are distributed and orientated as those of Tables 4 and 5, that is towards the vertical with an inward tendency from the edges. This tendency for the settlement to accumulate as well as to orientate in the direction of the light is more marked with the sparser settlements. The heavier settlements of Table 6 often obscure the increased settlement density towards the light, but an examination of the panels shows that the larger and presumably earlier settled individuals exhibit this tendency.

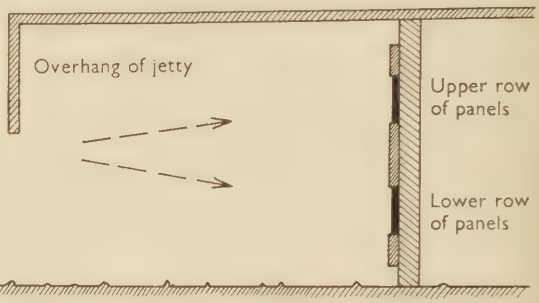


Fig. 7. Arrangement of frame exposed below jetty at M.T.L., Burnham-on-Crouch.

Gravity as the orientating factor would therefore seem to be ruled out, and any hypothesis dependent upon water currents seems unlikely. In contrast, all the evidence points to light as the factor concerned, and the fact that the test panels in the experiments described in this section were almost entirely sheltered from direct sunlight shows that

Table 6. *Analysis of the orientation of adult* Elminius modestus *settled on panels exposed at mid-tide level beneath wooden jetty, Burnham-on-Crouch*

Position	Date exposed	Date withdrawn	No. per sq.cm.	Percentage on upper half	Orientation (θ)	Resultant (R)
1	12 May 1949	10 Mar. 1950	9	44	+108·5°	0·23
2	5 July 1948	12 May 1949	1·4	30	−142·5°	0·29
3	5 July 1948	17 Oct. 1948	7	44	+129°	0·10
4	12 Aug. 1949	17 Nov. 1949	3·5	30	−164·5°	0·69
5	5 July 1948	4 Oct. 1948	7	40	−166°	0·62
6	5 July 1948	16 Aug. 1949	2·0	52	−164·5°	0·56
7	5 July 1948	19 Jan. 1949	3·7	42	−158°	0·67
8	5 July 1948	7 Sept. 1948	2·0	23	+143·5°	0·56
9	7 Sept. 1948	25 Apr. 1949	0·4	37	−138°	0·35
10	5 July 1948	19 Oct. 1948	6·5	50	+162°	0·54
11	5 July 1948	17 Oct. 1948	3·5	47	+175·5°	0·91
Mean				40	180°	0·45
12	5 July 1948	25 Apr. 1950	2·4	99	+ 3°	0·78
13	5 July 1948	19 Jan. 1949	1·0	94	+ 4·5°	0·82
14	5 July 1948	5 Oct. 1948	0·75	100	− 9°	0·73
15	5 July 1948	4 Oct. 1948	2·5	93	− 1°	0·92
16	5 July 1948	4 Oct. 1948	1·7	96	0·0°	0·91
17	7 Sept. 1948	4 Oct. 1949	8·5	51	+ 3°	0·79
18	21 Sept. 1948	24 Dec. 1949	8·5	52	− 16·5°	0·72
19	5 July 1948	5 Oct. 1948	2·1	80	− 15°	0·72
20	5 July 1948	19 Jan. 1949	2·9	79	− 20°	0·76
21	5 July 1948	15 Oct. 1948	0·8	96	− 5°	0·77
22	5 July 1948	4 Mar. 1949	1·9	96	− 8°	0·87
Mean				85	− 5·3°	0·79

orientation can be brought about in diffuse illumination.

Similar orientations have been noted in the case of *Balanus improvisus* and *B. amphitrite*. When settlements of *B. crenatus* and *B. improvisus* occur together it is usual to find *B. crenatus* commoner in deeper or darker situations, while *B. improvisus* settles nearer to the water-line or on submerged faces exposed to relatively high illumination or even intertidally; the orientation of *B. improvisus* is usually more marked than that of *B. crenatus*. *B. perforatus* resembles *B. improvisus* in settling predominantly at the water-line with a strong orientation in the direction of the light.

Further evidence that light is the main influence has been found on examining the orientation of *Elminius modestus* on vertical and horizontal panels exposed at West Mersea, River Blackwater, between 18 May and 15 July 1946 when a moderately heavy settlement of *E. modestus* took place. These panels were painted with a non-toxic composition and measured 30 × 10 cm. In the horizontal positions a heavier settlement took place on the under than on the upper surfaces, even at M.L.W.S. level. On the underside the settlement was most dense away from the support, i.e. at the end of the panel towards the incident light, while the settlement on the uniformly illuminated exposed upper surface showed no such effect (Fig. 8). Moreover, on the upper surface the orientation was on the whole random, while on the underside a marked orientation towards the light was apparent, this being stronger closer to the support where the light differential was greatest. Both the upper and lower surfaces, but more particularly the lower, showed a secondary orientation towards the edges of the panels. This

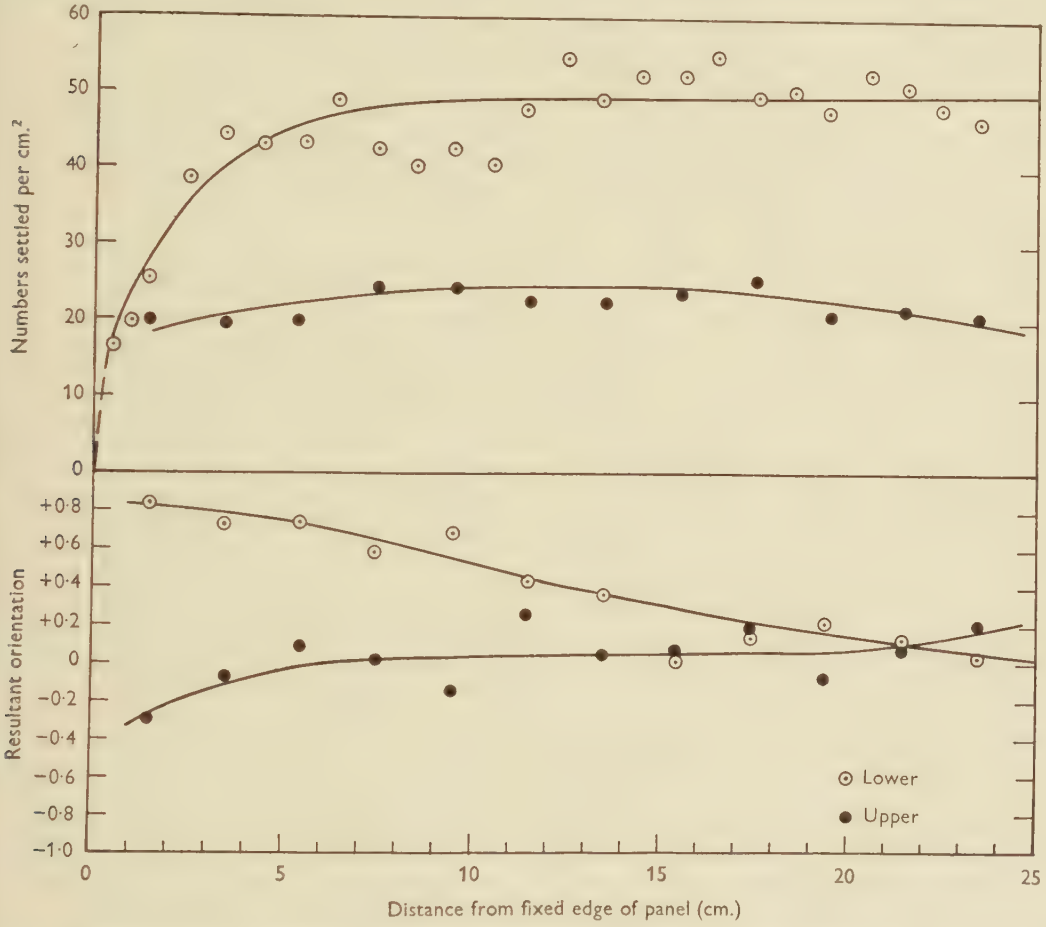


Fig. 8. Settlement and orientation of *Elminius modestus* on the upper and lower surfaces of a horizontally exposed panel supported at one end.

effect was exactly the opposite to that shown in Pl. 6, phot. 2, where presumably the shade offered by the 0·5 in. inset of the plates gave rise at the margins to an inwardly directed light gradient. It is natural therefore to relate this outward orientation to a gradient of increasing illumination towards the outer edges of the steel plates, and it is easy to appreciate that the under-side of a plane surface might be exposed to such an illumination gradient. But it should be noted that this would be dependent largely, if not entirely, on the Tyndall effect produced by suspended particles; turbidity is almost invariably present in the Essex estuaries where these experiments were conducted. However, an outward orientation on a plate exposed vertically to the light is also very commonly observed and cannot so readily be explained. Even the lower edges of vertically placed panels often show a reversal of orientation. It would be possible to assume that an illumination gradient initially absent might be set up in the course of settlement of a population in the following manner. If settlement occurs at random, then any point close to the edge of a plate will tend to have a greater settlement built up on the side away from the free edge because the closer to the free edge the less is the chance of an individual settling between this point and the edge. If the settlement of each individual produced an appreciable shading in the region around it, an illumination gradient will be formed towards the edge. This will have a particularly marked effect if the cyprid 'looks' along the plane of the surface, and a lesser effect if it takes in a wide angle of light.

In accordance with this theory, individuals settled later should be more randomly orientated than those settled earlier so far as the overall illumination is concerned, but should exhibit greater orientation towards the edges compared with those which settled first. This was tested by comparing the angular deviations from the mean of individuals of different size-groups from the centre of the underside of the plate described above (see Fig. 8). No differences could be detected, although the settlement was dense and offered every opportunity for a mutual shading effect (Table 1, p. 229).

An alternative theory may be offered which is more in accordance with the evidence of these experiments. We have noted that there is a tendency not only to orientate towards the light but also for the settlement to accumulate at first in neutral areas where two light gradients meet (see Tables 4–6). This may be interpreted as the result of migration of cyprids along the surface in the direction of orientation. Now even if orientation were initially at random but migration occurred more or less in straight lines or as a series of straight lines, the only individuals to reach the edges of a plate and settle there would be those which had a component of velocity, and presumably of orientation, in this direction, assuming that none could walk over from the reverse side. Thus an outward orientation would be produced at the edges which would extend inwards approximately to a distance equal to the mean straight path of the cyprid. The same effect of outwardly orientated individuals would be produced, but more intensely, if the direction of light were continually changing, provided that on ultimate settlement, the same orientation as was responsible for the migration is preserved. This is probably what happens in the case of panels exposed in open positions in the sea, where the direction of incident light is variable.

Direct correlation of orientation and light direction

In order to obtain a direct correlation in the field between the direction of incident light and the orientation of *E. modestus*, two plates, 10 × 30 cm., were exposed facing south (i.e. in the plane of the current) at Burnham-on-Crouch, one at M.L.W.N. and the other at M.T.L., in such a way that different parts of the plates received light from various directions, the fronts being illuminated and the backs shaded from above. The light incident on the plates from various directions was determined by means of a barrier layer type photocell connected to a portable micro-ammeter. A shade was placed over the photocell so that the incident illumination was restricted to a solid angle of approximately 45°. Readings were taken with the photocell pointing at 22·5° and 67·5° to the plane of the plate in eight directions fixed relative to the edge of the plate so as to cover as far as possible the whole solid angle of incident light. The readings were resolved to give the total illumination falling on each of the four quadrants in directions parallel to the edges of the plates. In all cases the determinations were made relative to the vertical incident light at times when the sky was completely obscured.

Table 7 shows the value of the light for different positions on the panel (defined by the horizontal (x) and vertical (y) co-ordinates (in cm.) from the top left-hand corner) expressed as (I), the percentage of total incident light on each of the four quadrants. The last column gives the ratio of the total resolved light to that recorded by the meter when placed horizontally in an unobscured position and thus offers a measure of the overall intensity of illumination at this point. Immediately below each value of the percentage of light falling in a given quadrant, is shown the percentage of individuals whose orientation lies within the same quadrant (O) estimated from points lying within 1 cm. of the point x, y and the total number of individuals in the

sample. In some cases x and y had to be chosen so that a reasonable sample would be obtained for orientation counts, otherwise readings were made in the middle ($x \simeq 5$) and at two points near each edge of the panel ($x \simeq 1, 9$), as well as at a series of positions along the length of the panel approximating to $y = 1, 5, 10, 20, 30$ etc. The correlation can be seen by inspection to be reasonably good. By taking the mean values of O for all quadrants over the ranges 0·0–0·1, 0·1–0·2, etc. in I, and plotting as in Fig. 9, the correlation is made more obvious. It will be noted that the line probably does not pass through the origin indicating that even when the fraction of light in a given direction

Table 7. *Correlation of light and orientation for* Elminius modestus

(Fraction of light indicated by L; fraction of orientation indicated by O.)

			Quadrant OA $-45°$ to $+45°$	Quadrant OA^1 $-135°$ to $+135°$	Quadrant OB (E) $+45°$ to $+135°$	Quadrant OB^1 (W) $-45°$ to $-135°$	Totals (see text)
Panel at level of mean low water, neap tides:							
Front (exposed)							
x (cm.)	y (cm.)						
3	2	L	0·64	0·07	0·08	0·22	1·29
		O	0·80	0·00	0·00	0·20	30
8·5	4	L	0·70	0·50	0·10	0·15	0·96
		O	0·84	0·50	0·00	0·11	18
6	11	L	0·59	0·07	0·21	0·12	0·56
		O	0·72	0·04	0·15	0·09	80
6	20	L	0·32	0·10	0·32	0·26	0·31
		O	0·41	0·15	0·33	0·11	27
6	29	L	0·26	0·09	0·31	0·34	0·28
		O	0·39	0·21	0·24	0·15	33
Back (shaded)							
x	y				(W)	(E)	
8·5	5	L	0·14	0·23	0·43	0·20	0·16
		O	0·06	0·34	0·32	0·28	71
6	18	L	0·23	0·22	0·34	0·23	0·30
		O	0·09	0·50	0·18	0·23	22
5	30	L	0·25	0·24	0·26	0·25	0·35
		O	0·19	0·35	0·33	0·13	65
Panel at mid-tide level:							
Front (exposed)					(E)	(W)	
3	4	L	0·47	0·04	0·30	0·19	1·85
		O	0·77	0·00	0·04	0·19	26
8	7	L	0·57	0·04	0·27	0·10	1·4
		O	0·79	0·00	0·07	0·14	14
4	14	L	0·71	0·08	0·15	0·05	0·75
		O	0·60	0·05	0·20	0·15	20
5	23	L	0·60	0·08	0·25	0·09	0·63
		O	0·49	0·05	0·22	0·24	94
Back (shaded)					(W)	(E)	
5	5	L	0·09	0·21	0·12	0·28	0·017
		O	0·14	0·12	0·28	0·47	43
6	15	L	0·27	0·08	0·08	0·57	0·12
		O	0·05	0·12	0·07	0·75	56
5	20	L	0·26	0·08	0·12	0·54	0·14
		O	0·03	0·26	0·03	0·68	38
5	25	L	0·26	0·08	0·26	0·40	0·20
		O	0·14	0·43	0·05	0·38	37

is on average only one-tenth of the total a small number of individuals may take up this orientation.

The effect of edge orientation in this experiment was very clear and is demonstrated in Table 8. The fraction of individuals per degree × 360 falling

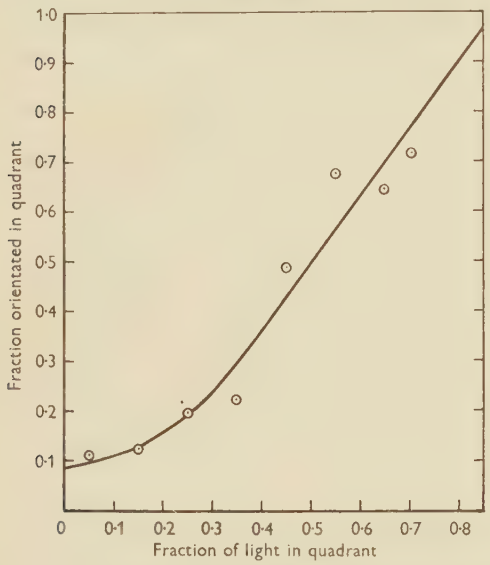


Fig. 9. The relation between the fraction of light falling in a given quadrant and the fraction of individuals (*Elminius modestus*) orientated in the same quadrant.

within the angular range given in the columns is shown for the centre and two edges of each face, the numbers having been added for all values of y. For a random orientation the most probable value is unity, hence this figure is a measure of the number found compared with that expected. The edges are recorded as east and west, in order to indicate that the shift in orientation is not due to any external orientating effect such as current or light but is simply due to the proximity of the group to the edge of the plate.

Thigmotropic orientation

Both *E. modestus* and *Balanus balanoides*, and probably also many other species, show well-defined orientation in relation to cracks, grooves and ridges, independent of the overall direction of light. If a series of grooves is exposed to settlement, not only are the grooves subjected to preferential settlement, but the orientation is strongly defined along the groove (Pl. 6, phot. 3). This applies not only to grooves of the same order of size as the cyprid but also to shallower grooves of large size and even to fine scratches. The orientation in large deep grooves may well be due to the orientating effect of light falling mainly along the direction of the groove, but orientation in very shallow grooves must probably be ascribed to a tactile or thigmotropic response.

THE NATURE AND POSSIBLE FUNCTION OF ORIENTATION

No evidence has been presented as to the precise nature of the reaction to light or at what time during settlement it is effective. Direct observations on

Table 8. *Effect of edge orientation* (Elminius modestus)

Number present/number expected

Position	West facing						East facing						
	±180°	135°	90°	60°	40°	20°	0°	20°	40°	60°	90°	135°	S.D.
M.L.W.N. front:													
West edge	—	0·14	0·38	**1·83**	**2·62**	**5·87**	**3·27**	**2·29**	0·32	0·26	—	—	0·47
East edge	0·48	0·18	—	0·32	0·80	**1·60**	**4·40**	**4·40**	**2·00**	**1·28**	0·43	0·18	0·52
Centre	0·73	0·46	0·55	0·82	0·41	**1·65**	**1·44**	**2·67**	**2·46**	**1·80**	0·87	0·46	0·27
M.L.W.N. back:													
West edge	0·34	**1·63**	**1·76**	**3·83**	**2·20**	**1·47**	0·74	0·37	—	—	—	0·34	0·49
East edge	0·30	**1·06**	0·90	0·54	—	0·34	0·34	**1·02**	**2·04**	**2·44**	**1·27**	**1·51**	0·48
Centre	0·85	**2·00**	**1·37**	**0·77**	**1·28**	0·96	0·00	**1·28**	0·51	0·68	0·57	0·85	0·46
	±180°	150°	120°	90°	60°	30°	0°	30°	60°	90°	120°	150°	
M.T.L. front:													
West edge	—	0·52	0·52	0·26	**1·30**	**3·65**	**2·87**	**2·35**	0·52	—	—	—	0·51
East edge	—	—	0·35	—	0·70	—	**2·12**	**4·57**	**2·82**	**1·06**	0·35	—	0·59
Centre	—	0·21	0·43	0·64	**2·02**	**2·76**	**2·87**	**1·49**	0·85	0·53	0·11	0·11	0·31
M.T.L. back:													
West edge	**1·02**	**1·02**	**1·02**	**2·40**	**3·07**	**1·71**	0·34	0·34	0·34	—	0·34	0·34	0·59
East edge	—	—	—	—	—	—	—	—	**1·60**	**7·20**	**3·20**	—	0·89
Centre	0·75	**1·24**	0·34	0·25	0·34	0·58	0·41	0·33	**1·74**	**2·48**	**2·15**	**1·41**	0·29

Figures which exceed unity (see text) are printed in heavy type.

cypris larvae settling from the sea have not been made, but under artificial conditions cyprids of *B. balanoides*, *B. crenatus* and *Elminius modestus* have been observed to crawl towards the light, adhering and pulling along the body at each step by means of the antennules. Settlement has been observed in *Balanus balanoides* (P. N. J. Chipperfield, personal communication) and in *Elminius modestus* by one of us (D. J. C.). In both cases the cyprid, before settlement, executed exploratory movements, including pivoting by the antennules and rotating the body from side to side, finally pouring out a flat disk of opaque cement before becoming immobile. Distances of several centimetres may be traversed by the cyprid before settlement; alternatively it may leave the surface and swim. These observations agree with those of McDougall (1943) and Pyefinch (1948) rather than with those of Visscher (1928). However, in the case of the earlier naupliar stages at least, a positive response to light, though usual, is not shown invariably. If a group of, say, *Balanus crenatus* Stage II larvae is placed in strong illumination, the majority of the larvae react negatively, whereas in poor illumination they may all react positively. If an intermediate illumination is used they frequently divide into two groups which retain their individual positive or negative response when removed to another dish under similar conditions. The first- and second-stage nauplii may to some extent be differentiated in this way, since the first-stage are very slightly more strongly photo-positive than the second-stage nauplii. According to Groom & Loeb (1890) diurnal fluctuations of the light reaction also take place. The light reaction therefore appears to be generally positive throughout the larval life, but is dependent upon the conditions of illumination and perhaps also on the physiological state of the organism (Ewald, 1912).

In considering the function of the orientation with regard to settlement, two possibilities ought to be considered: either that it has a direct function in providing the adult barnacle with some advantage, or that it is a vestige of a light reaction of functional significance only in the earlier stages. Taking the first alternative, can orientation as such give any advantage in feeding, growth, reproduction, or survival of the adult? The first two possibilities have already been clearly negated. With regard to reproduction, although copulation is essential in many species, individuals lying at different orientations appear to be equally likely to be inseminated, as barnacles in all possible orientations may be observed to contain fertilized eggs at certain seasons. An individual acting as a male has, moreover, been observed to inseminate surrounding individuals in various positions, the penis being sufficiently long and flexible. Lastly, since no differential mortality has been observed between individuals of anomalous orientation, it is also unlikely that better survival is achieved by the cirri beating downwards. There is no evidence, however, that the normal orientation with the cirri beating away from the light may not confer some advantage by enabling the adult to respond more readily when shaded by a moving object, as for example a predator (the well-known 'shading reaction'). (According to Fales (1928) the adult possesses paired photo-receptors, derived from the median eye of the cyprid, on the inside of the shell close to the suture between the rostral and the lateral plates.) The effect, if any, appears to be of little survival value in these species.

Taking the second alternative, there is ample evidence that a positive reaction to light is directly advantageous in the early stages. It may play a part in dispersing the newly hatched larvae into the plankton and in maintaining them in this environment away from the sea bottom during the main part of the larval life.

Some benefit, moreover, may accrue to the adult as a result of a positive response to light during the migratory phase of the cypris larva; such an advantage, however, is not necessarily related to its final orientation. It has been shown that *Chthamalus stellatus* grows faster and produces more frequent broods in positions exposed to greater water flow (Crisp, 1950); such positions as an exposed edge or prominence are especially favourable, while deep fissures or enclosures offer poor growth sites where silting often results in high mortality. This applies also to *Elminius modestus*, *Balanus amphitrite* and probably to other cirripedes (unpublished observations by D. J. C.). A migration towards the light will thus tend to bring the cyprids into these more favourable environments and so will indirectly affect the survival and reproduction of the adult barnacles.

On the whole, therefore, the orientation effect appears likely to be a result of the light reactions of the larva, which persist up to the time of settlement. This is a more acceptable view than that it is a specialized behaviour pattern of unknown function operating specifically at the time of settlement.

The existence of a negative reaction in strong illumination can also be related both to the needs of the larva and to its settling behaviour. It is well known that in raft tests barnacles are found in smaller numbers in well-illuminated positions near the water-line than in similar positions where shade is provided. This is true of bare surfaces and is therefore independent of algal exclusion which exercises a similar effect. It also applies more particularly to sublittoral forms such as *B. crenatus* and to a lesser degree *B. improvisus* than to *B. balanoides*,

B. perforatus and *Elminius modestus* which occur intertidally. This general choice of illumination, like other discriminatory effects, is sometimes masked by heavy settlements; nevertheless, it represents a mechanism which maintains the cyprid at a level most suitable for attachment in its ultimate habitat. Furthermore, a cyprid showing an indiscriminate positive reaction to light would be liable to reach the surface of the sea, where it might become stranded on the surface film, as frequently occurs when cyprids are placed in shallow dishes. This is due to their possessing a hydrophobic surface. After settling, however, a positive reaction appears to be the general rule.

In the case of intertidal species in particular yet another hazard must be considered, that of being swept off by wave action or by abrasion. Clearly this must act in the directly opposite sense from the hazard due to silting up or remaining in a 'stagnant' habitat. The best compromise would be a rough surface providing a key for attachment in an exposed position. The strongly marked thigmotropic reaction which comes into play, presumably by initiating the cementing process, when the cyprid is located in a groove or against a ridge (but not on the outside of a ridge or angle) ensures such a good key. Thus, according to this hypothesis, migration and exploration continues in a direction mainly towards the light source until the settling or cementing reaction comes into play. This reaction may be initiated by contact with a suitable obstacle or groove, but even in the absence of such a suitable obstacle it eventually supersedes the migratory phase. This would be in accord with many other examples of instinctive behaviour where, if the requisite stimulus is not received, a gradual reduction in discrimination occurs until the behaviour pattern takes place spontaneously. This is further borne out by the frequently observed lack of discrimination on the part of heavy settlements of cyprids, where only a small proportion come into immediate contact with desirable sites, compared with the remarkable discrimination shown by sparse settlements. Certain species do, however, regularly show greater discrimination than others. It is interesting to observe that the thigmotropic reaction appears to be most clearly shown by the two purely intertidal species, *Balanus balanoides* and *Chthamalus stellatus*. The former rarely, and the latter never, settle on plain glass surfaces, whereas *Elminius modestus*, *Balanus perforatus*, *B. improvisus*, *B. amphitrite* and *B. crenatus*, which all extend into the sublittoral, settle readily on smooth surfaces. Clearly smooth surfaces, such as occur on mobile beach pebbles, would be most undesirable for intertidal forms.

To what extent water currents and wave action affect settlement either by rheotropic or direct mechanical effect has not been directly tested in these experiments. In view of the conformity of our observations under conditions where current, etc., was not controlled in any way, with such a theory as is outlined above involving only light and thigmotropism, it appears likely that water movement usually exercises only a minor influence.

SUMMARY

1. A review of existing literature leaves doubt as to the reactions of the cypris larva at the time of settlement, and possible changes in its orientation subsequent to metamorphosis.

2. Observations are recorded on a number of species, but experimental work is restricted to *Balanus crenatus* and *B. balanoides* settled on panels continuously submerged from a raft at Millport, and *Elminius modestus* settled on panels exposed intertidally in certain Essex estuaries.

3. Young and adult barnacles are similarly orientated, and in these three species no rotation occurred during growth after metamorphosis.

4. No significant differences of growth-rate were found between groups of barnacles having different orientations either for *Balanus crenatus* or *B. balanoides*.

5. The orientation of these barnacles is dependent on the direction of the incident light at the time of settlement. With all three species under conditions of vertical illumination and moderate population density the tendency for the carino-rostral axis to be vertical, with the cirri beating downwards, is shown by frequency-orientation-angle histograms. *Elminius modestus* was collected on inset panels, on horizontally exposed panels and on vertical panels where the light did not fall from above. In all cases detailed analysis shows that the direction of incident light is the controlling factor.

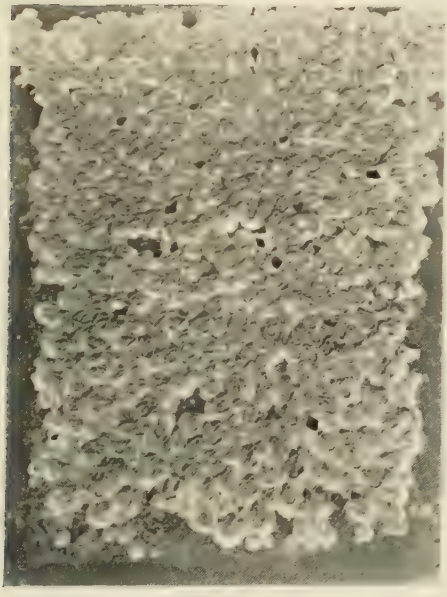
6. A direct correlation between the orientation of samples from settled populations, and the direction of incident light as measured by a photometer, has been demonstrated for *E. modestus*.

7. Orientation towards the free edges of panels which are not inset is commonly observed and is probably the result of migration towards the light before settlement.

8. A thigmotropic settling reaction is strongly developed in intertidal species. This reaction is evoked by the presence of obstacles and grooves, and orientation usually occurs along the direction of the groove.

9. Two alternative functions of the light orientation are suggested: either that it may provide the adult barnacle with some direct advantage, or that it may be a vestige of a reaction which is functional only in the larval stages before metamorphosis. The latter alternative is considered more acceptable.

1



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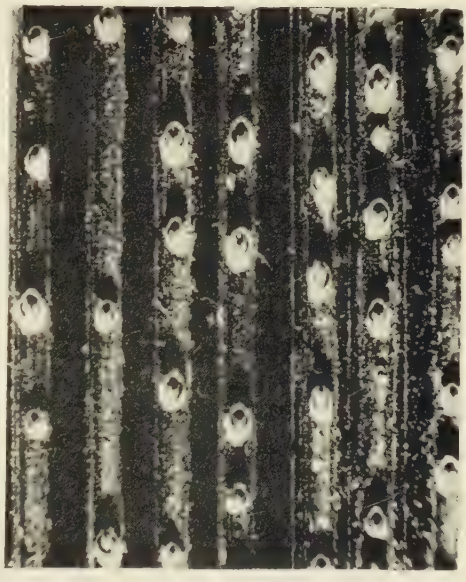

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Phot. 1. Exposure frame at mean low water, Burnham-on-Crouch, showing method of mounting and the small inset panels used for settlement of *Elminius modestus*.

Phot. 2. *Elminius modestus* showing inward orientation on an inset panel.

Phot. 3. Orientation of intertidal *Balanus balanoides* in grooves.

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A NOTE ON THE PAPERS OF ELTON AND WILLIAMS ON THE GENERIC RELATIONS OF SPECIES IN SMALL ECOLOGICAL COMMUNITIES

By T. B. BAGENAL
The Marine Station, Millport

The Easter Symposium of the British Ecological Society on 'The Ecology of closely allied species' (Anon. 1944) considered Gause's contention (1934) that two species with similar ecology cannot live together in the same place. Elton published his contribution to this meeting in an expanded form (Elton, 1946), giving an analysis of 55 animal and 27 plant communities, and calculating the number of species per genus for each community, the average of which was found to be 1·38 for animal, and 1·22 for plant communities. Elton also considered the number of species per genus in faunal lists, taking *A check list of British insects* (Kloet & Hinks, 1945) as an example. In this case he calculated the number of species per genus to be 4·23. He attributed (p. 66) 'the difference in species/genus frequencies between ecological surveys of relatively small parts of any general habitat, and those for faunal lists from larger regions,...to existing or historical effects of competition between species of the same genus, resulting in a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to co-exist permanently on the same area of the same habitat.'

This paper was criticized by Williams (1947) who, using a statistical method based on the logarithmic series, re-analysed 13 of Elton's communities and showed that they contain fewer genera than would be expected in a sample of the same number of species taken at random (i.e. independent of generic relations) from a suitable fauna or flora list. This, he concluded (p. 17), 'can only be interpreted as a natural selection—in the course of time—in favour of species in the same genus rather than against them. It is possible to suggest reasons for this—for example, if one species in a genus is capable of survival in a given physical environment, it seems likely that other species in the same genus might be more likely to have a similar genetic make-up than species in another genus, and so might have a good chance of survival'

Before attempting some closely related work, it was found necessary to attempt a reconciliation between these two conflicting views, and the present note is the result of a consideration of the thirteen communities used by both Elton and Williams from the point of view of their suitability for the type of analysis to which they have been subjected; from this consideration three important points have emerged.

First, the habitats of many of the communities are very heterogeneous, in some cases including species from several totally dissimilar minor habitats. For example, the list analysed as community 20 (community numbers refer to Table 1, p. 55 of Elton, 1946) was compiled from samples taken from five stations chosen over a 50-mile stretch of the River Wharfe (Percival & Whitehead, 1930). The distances between adjacent stations varied from 6 to 26 miles; and from the first station at Grassington to the last at Ullskelf the river changes from a fast-flowing mountain river with a rocky bottom, to a placid alluvial lowland river. The list on which community 12 was based was derived from a survey by Pyefinch (1937) of eight pools on Bardsey Island, ranging from brackish to fresh-water conditions. Pyefinch stresses (p. 137) 'the great variation in the environment from one pond to another, as each is influenced to a considerable extent by purely local conditions'. Indeed he states (p. 117) that the ponds were 'so chosen that the full range of environment was adequately represented'. Similar criticisms apply to community 13 (Laurie, 1942) and also to community 14 (Humphries, 1936) where, in the original survey, particular attention was paid to two stations as they represented physiographically different habitats.

In these cases Elton and Williams have considered the occupants of a variety of habitats as constituting one community, even when the authors of the original papers have gone out of their way to stress that the sampling stations were chosen expressly because of their dissimilarity. Both authors were interested in animals living together in one habitat in competition with each other, so that the choice of many of the communities, especially the Bardsey Ponds with their great physical and chemical differences making them quite unsuitable for the type of analysis to which they were subjected, was particularly unfortunate.

Secondly, it should be noted that the animals in the original lists were often collected by means of a variety of sampling devices. For example, the

upland pond of community 13 (Laurie, 1942) was sampled by using a hand-net, a dredge, and by examining the contents of a square of the bottom of the pond 15 × 15 in. to depth of 18 in. As it is unlikely that animals obtained by these methods would compete with one another or live in the same ecological 'place', they do not provide data relevant to either Elton's or Williams's arguments. The same criticism applies to community 22 (Laurie & Jones, 1938).

The final point that emerges from a consideration of the original papers on which the communities were based is that some of the lists are of communities that have been sampled over a long period of time. In fresh-water habitats the seasonal variations in the fauna and flora may be very great; a point which was considered in the paper on which community 20 was based. This particular list was the result of collecting over a period of one and a half years. The upland pond of community 13 was sampled during July and October of 1940, and April, July and August of 1941. In these examples the species may be prevented from competing by one or more factors that are dependent on time, of which temperature, light intensity, turbidity, rate of flow and flooding, and the amount and kind of vegetation are the more obvious. Percival & Whitehead emphasize that the character of the associated fauna in the River Wharfe is largely related to the length of the life cycles of the animals and the duration of the period when the mature adults are found, and that these are related to the temperature.

It will be noted that only five of the thirteen of Elton's communities that Williams also analysed have been considered here. They have been chosen particularly because they are the most unsuitable; however, the same criticisms apply to the other eight communities, although less forcibly.

Williams (1947) continued by comparing the Index of Diversity of a number of communities with the appropriate fauna or flora list representing the larger population from which the community had been selected. He found that the smaller communities had not only a lower number of species per genus but also a lower Index of Diversity, indicating a selection in favour of species of the same genus rather than against. The communities he used were different from those used by Elton, partly because the latter were not suitable owing to the fact that in general the number of species was too small: no community with as few as 30 species will give statistical data suitable for analysis by a logarithmic series.

Williams's communities are, for the same reasons, as unsuitable for analysis as are those of Elton. For example, community *b* (community letters refer to sect. 4, p. 14, of Williams, 1947) was taken from a list of the flowering plants of Scolt Head Island, Norfolk (Chapman, 1934). The area of this island is about one and a half square miles and includes the following habitats: shingle, dunes, lows, eroded dunes, marshes and the shore itself. The vegetation has been modified in places by rabbits, sheep, man, and planted pines and shrubs. Communities *f* and *g* are taken from lists of the Capsidae (Bedwell, 1945) and Lepidoptera (Foster, 1937) respectively, of Hertfordshire. Both contain the results of collecting over a considerable period (since 1828 in latter case) and both must inevitably contain species from a very wide range of habitats. In the original paper on which community *d* is based ('The Lepidoptera of Wicken Fen, Cambridge'; Farren, 1936: 258), it is stressed that 'The large number of species in the list in no way peculiar to a fen habitat is not necessarily attributable to the inclusion of the cultivated part of Burwell Fen, as most of them have been observed in other parts of the district, and many on the Sedge Fen itself.' Farren (p. 259) also gives some examples of species typical of different habitats. 'There are species quite foreign to a fen habitat, such as *Oeonistis quadra* L., *Ptilophora plumigera* Esp., *Metrocampa dolobraria* L., and others. At the same time they are not more remarkable than *Drepana binaria* Hufn., and *Geometra papilionaria* L., two birch wood species which I know were taken on some small birches in the heart of the Sedge Fen, and a specimen of *Agrotis praecox* L., a coast species which I knocked out of the thatch of a barn on the edge of Burwell Fen.' These extracts emphasize the difficulties inherent in the use of published lists, since there is no indication concerning which species belong to the habitat and which are chance vagrants from a totally unrelated one. Unless such a distinction is made, conclusions based on the assumption that the list is of species living in one habitat, may give erroneous impressions. It has already been mentioned that communities *f* and *g* were the result of collecting over a long period. This is also the case with community *a* (Brenchley & Adam, 1915), which is based on a list of plant species found on about half an acre of abandoned wheat field in four surveys between 1886 and 1913.

Williams admits (p. 16) that of these communities, 'None of them is very small.' It is likely that most ecologists will agree that the county of Hertfordshire is not a very small habitat (from the point of view of a moth); nevertheless, it would appear reasonable to suppose that for a consideration of Gause's contention that two species with similar ecology cannot live together in the same place, and also for the study of related species competing for limited density dependent resources, it is very small habitats that require the closest attention.

Williams explains (1947) his choice of habitats by saying '. . . as we have already explained that in the very small communities the chance of getting two species in one genus is too low to be the basis of discussion'. This admission appears to destroy his whole thesis and to contradict his conclusions that there is selection in favour of species of the same genus exploiting the same habitat. What is really meant is that in very small communities his method of analysis is too insensitive to handle data relevant to Gause's hypothesis.

The principal difference between the two authors appears to be in their use of the word 'habitat'. In Gause's hypothesis the word 'habitat' should surely be used in its narrowest sense and be equivalent to 'microhabitat'. When this meaning of the word is understood, although much of his evidence is not strictly relevant, Elton (1946, p. 66) is correct in his conclusion that there is '. . . a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to coexist permanently on the *same* area of the *same* habitat' [my italics]. Williams used a method of analysis which by requiring a large number of species from a single 'habitat', precluded the use of data strictly relevant to Gause's hypothesis (and Elton's conclusions, although he was still able to use some of Elton's data), and required the use of 'habitat' in a much broader sense. When this much broader use of the word 'habitat' is understood, Williams's conclusions are correct, but far from contradicting Gause's hypothesis they appear to form an interesting corollary to it, namely that closely related species are more likely to be found in *similar*, though not identical, habitats, than are totally unrelated ones. That is, the same ecological niche in similar habitats is more likely to be occupied by related species than by unrelated ones; and conversely, that related species are more likely to occupy the same niche than a different one. When Williams's communities were large enough to contain more than one example of the same niche, there were more species per genus than would be expected, and when the communities were small (community *c*, plots 9 and 10; Brenchley, 1924) he found that each species was in its own genus.

This rather obvious corollary to Gause's contention is supported not only by the concept of an 'ecological niche', but also by the present theories of speciation, because a species will not evolve into two related species unless there is some isolation, either geographical, ecological or genetical, which separates two stocks of the parent species. It is likely that when two new related species have evolved they will have *similar* ecological requirements and occupy the same niche, but it is unlikely that they will exploit the *same* resources, of the *same* habitat.

The author is indebted to Dr D. T. Gauld for help and general criticisms in the preparation of this paper.

SUMMARY

1. The original papers on which Elton (1946) and Williams (1947) based their communities have been examined with regard to Gause's (1934) hypothesis, and from the point of view of their suitability for the type of analysis to which they have been subjected.

2. It is shown that many of the communities are quite unsuitable owing to one or more of the following reasons: (*a*) the 'habitat' was very heterogeneous, (*b*) the community was sampled by a variety of sampling devices, and (*c*) the community was sampled over a long period of time.

3. It is suggested that the present confusion is based on differences in the meaning of the word 'habitat', that with Gause it is synonymous with 'microhabitat', while with Williams it has a much broader meaning. From this standpoint Elton's conclusions appear to be correct, though based on unsuitable data, and Williams, far from contradicting Gause and Elton, has provided the corollary that related species are more likely to be found in *similar*, though not identical, habitats than are unrelated ones.

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INTRA-GENERIC COMPETITION AS ILLUSTRATED BY MOREAU'S RECORDS OF EAST AFRICAN BIRD COMMUNITIES

By C. B. WILLIAMS

Rothamsted Experimental Station, Harpenden

In this *Journal* in 1947 (Williams, 1947) I brought forward evidence which seemed to support the idea that, among the factors affecting the survival of species in any animal or plant community, the advantages of close relationship, as indicated by belonging to the same genus, were of greater average importance than any associated drawbacks.

The argument developed was that if the frequency distribution of genera with different numbers of species is known for a larger area enclosing and including the smaller community under consideration, then it is possible to calculate how many genera should be represented in a random* sample of species from the larger area containing the same number of species as that found in the special community. If the species in the community are actually contained in this number of genera, then there is no statistical evidence that generic relationship has been associated with the survival of species in the community. If there are too many genera, then close generic relationship has been a drawback to survival. If, on the contrary, there are too few genera in the natural population, the generic relationship must on an average be advantageous.

Out of sixteen examples from the British Isles, eight for animals and eight for plants, that I gave in the paper quoted, all but one showed too few genera; one showed the same number; and no community showed more genera than would have been expected by chance.

My interpretation of these facts has been criticized chiefly by the statement that the communities or associations considered were too large and were capable of subdivision, so that the congeneric species were not really filling the same 'niche'. There is, however, no limit to which one can divide a habitat into niches or micro-climates, so that by making the niche small enough it is always possible to show that no two species, whether congeneric or not, can co-exist.

What my figures indicated was that as a larger and more complex community is split up into smaller and less complex communities, the number of congeneric species appears to increase above the expected rather than to decrease; or in other words the 'generic diversity' decreases. Once the size of the community has been reduced to a level when one would not, by chance, expect any congeneric species, then their absence cannot be used as an argument either *for* or *against* the idea of intra-generic competition.

In the above paper the measurement of generic diversity was based on the assumption (supported by evidence) that the frequency distribution of the number of genera with different numbers of species was in or close to the Logarithmic Series. Simpson (1949) showed that it is possible to calculate a simple measure of Diversity which is independent of any assumption about the mathematical expression of the frequency distribution.

Simpson argued that in any community consisting of a number of species (N) classified into genera the total number of different ways in which two species can be selected at random from the population is

$$N(N-1)/2;$$

while the number of ways in which 2 species can be selected belonging to the same genus is

$$\Sigma n(n-1)/2;$$

where the successive values of n are the number of species in each genus.

Thus the chances that 2 species selected at random should belong to the same genus are

$$\frac{\Sigma n(n-1)}{N(N-1)}; \text{ or 1 chance in } \frac{N(N-1)}{\Sigma n(n-1)}.$$

This latter figure is a measure of the 'Generic Diversity' of the population.

For example if a population consisted of 10 species with 1, 2, 3, 4 species in each of 4 genera then the number of possible pairs is $10 \times 9/2 = 45$, and the number of possible pairs belonging to the same genus is

$$\frac{(2 \times 1) + (3 \times 2) + (4 \times 3)}{2} = 10;$$

therefore the chance that 2 species selected at random would belong to the same genus is 10/45 or 2/9; and the Generic Diversity is 4·5.

In a recent volume of this *Journal*, R. E. Moreau (1948) has discussed the distribution of 172 species

* By 'random', in this connexion, is meant without respect to generic relationship.

of birds, belonging to 9 families of Passerines, in the Usambara Hills of north-east Tanganyika, with special reference to the occurrence of 2 or more species of the same genus co-existing in a single ecological association or community. He shows that there are a number of such cases, but that in many of them the related species have different habits which prevent them competing with each other: they occupy different 'niches' within the community.

While admitting the probable correctness of these explanations I think that it will be of value to study his data from a statistical point of view, because no attempt was made to show whether or not the number of such cases was larger or smaller than might be expected by chance; and also because Moreau's data, being the results of observations by a field ecologist who is familiar with his terrain and his birds, are likely to be as good as it is possible to get anywhere for such an analysis.

Moreau informs me that these 9 families were selected for particular study because they were the largest families which he considered that he knew adequately. Within these families all species and genera are listed so that there is no selection for generic size. He recognized 172 species of birds in 92 genera, and he subdivided his area into 32 different ecological types. The following are the numbers of genera with different numbers of species in the whole population:

Species/genus ...	1	2	3	4	5	6	7	8	9	10
No. of genera ...	51	24	10	2	—	3	1	—	—	1

The number of genera and species in each of the 9 families and subfamilies recognized by Moreau is shown at the foot of Table 2, where the names of the groups can also be found.

Table 1 shows the classification of Moreau's 32 ecological habitats; Table 2 shows the distribution

Table 1. *Moreau's classification of the ecological habitats*

1. Lowland (0–2500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Riverine forest	(1) Trees
	(2) Ground-stratum
(*c*) Wooded grassland	(1) Grass
	(2) Trees (deciduous)
	(3) Low semi-evergreen bush
	(4) Tall clumps, semi-green bush
(*d*) Semi-desert thorn country	(1) Trees and bushes
	(2) Ground, including woody herbage
	(3) Riverine strips
(*e*) Induced vegetation	(1) Trees and tall bushes
	(2) Dense low bush
	(3) Herbaceous cover
	(4) Scanty cover
(*f*) Swamp	
2. Intermediate level (2500–4500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Grassland	
(*c*) Induced vegetation	(1) East Usambara (humid)
	(2) West Usambara (semi-humid)
(*d*) Swamp	
3. Highland (4500–7500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Moorland	
(*c*) Induced vegetation	

Table 2. *Moreau's data on bird distribution in Usambara Hills, Tanganyika, rearranged to show number of species in different habitats*

Moreau's habitat no.	Capitonidae I	Pycnonotidae II	Muscicapidae III	Turdidae IV	Sylviidae V	Prionopidae and Laniidae VI	Nectariniidae VII	Ploceidae: Plocainae VIII	Ploceidae: Estrelidinae IX
1 *a* 1	C_1 C_2 D E_2	—	A_2 F	—	G_5	B_2	F_3	—	—
2	—	B_3	J_1 L_1	—	G_2	—	E F_4	A_1	—
3	—	B_4 B_5	—	C G_2 M	—	O	—	—	D
4	—	F G	B F H M_1	—	L	G_1 L	F_1 F_6	—	G H
b 1	A_2	—	—	—	—	—	—	—	—
2	—	B_1 B_2 B_6	K	—	—	—	—	—	—
c 1	—	A	—	—	M_1 M_4 M_5 M_6	—	—	—	A_1 P
2	A_1 E_1	—	G_1 D J_2	—	K_1	B_1 K_1	A_1 C_1 D_2 D_4	C	—
3	—	E	—	K_1 K_2 L_1	J_1	F_3 H_2	—	—	—
4	—	D	G M_2	G_1 L_3	—	G_1	—	—	—
d 1	B	—	C_2 J_3	—	G_4 J_1 K_2	A C D E_2 G_2	D_2 F_5	A_5	—
2	F_2 F_3	—	—	A_2 D L_2	F G_6	F_1 N	—	—	C F M_2 N_2 Q
3	—	—	—	K_2	—	—	A_2	A_4 A_6 A_7 A_9 A_{10} D_1 D_2 E_1 E_2 E_3 F G_1	M_3
e 1	—	A	G M_2	—	—	G_3 M	C_1 D_1 F_1	A_6 A_7 A_9	—
2	—	D	K	G_1 K_1 K_2 L_3	—	F_3 H_2	—	A_8	—
3	—	—	—	—	M_1 M_4 N O P	—	—	D_1 D_2 G_2 E_1 E_2 E_4	A_1 P
4	—	—	—	A_1	—	—	—	—	K_2 N_1
f	—	—	—	—	A C D	—	—	B	—
2 *a* 1	C_1 C_2 D	—	—	A_3	—	K_1	—	A_2	—
2	—	B_3 C_3	J_1 L_2	—	B G_2	—	E F_4	A_1	—
3	—	B_4 B_5 B_7	—	B C H J_1 M	D_2 G_3	O	—	—	D E
4	—	C_2 F G	A_1 M_1 H	—	H L	F_3	F_1 F_2	—	H
b	—	—	—	F	C E M_6 O	—	—	—	—
c 1	—	A	A_1 E J_2	G_1	M_3 P	E_1 F_3 H_1 J	D_1 F_1	A_3 A_8 B	A_2 B L M
2	F_1	—	D	G_1	M_3 P	E_1 F_3	C_2	A_3 B	L M_1
d	—	—	—	—	C E	—	—	B	—
3 *a* 1	C_1 D	—	—	A_3	—	K_1	—	A_2	—
2	—	C_1 C_2	L_2	—	B G_2	—	E	—	—
3	—	B_4 B_5	—	B H J_1 J_2 M	D_2	F_2	—	—	E
4	—	C_2	A_1	—	D_1 G_1 H	F_3	C_3	—	—
b	—	—	—	F G_3	D_1	—	A_1 B	—	—
c	—	—	E	F G_3	—	E_1	A_1 B C_2	A_3	L M_1
No. of genera	6	6	12	12	15	14	6	7	14
No. of species	11	15	18	20	28	21	17	21	21

Capital letters represent the genera in each family and the subscript numbers the species, if more than one in the genus, according to Moreau's system.

of the species, genera, and families among the habitats; and Table 3 shows the number of species, and the number of genera with 1, 2, 3, etc., species in each of the habitats. One or two misprints in the original tables have been corrected with the co-operation of Mr Moreau.

A preliminary study of the total population of 172 species in 92 genera and 9 family or subfamily divisions gives us the following information:

(1) The total number of ways in which 2 species can be selected from the 172, is $172 \times 171/2 = 14706$.

(2) The number of ways in which 2 species can be selected so as to belong to the same genus is

$$(24 \times 1) + (10 \times 3) + (2 \times 6) + (3 \times 15) + (1 \times 21) + (1 \times 45) = 177.$$

(3) The number of ways in which 2 species can be selected so as to belong to the same group (family or subfamily according to Moreau's grouping) is $\frac{1}{2}(11 \times 10 + 15 \times 14 + 18 \times 17 + 20 \times 19 \ldots) = 1647$: this of course includes the 177 cases where they are in the same genus. Thus of the 14706 ways in which 2 species can be selected at random from the original population:

in 177 they will be in the same genus;
in 1470 they will be in the same family but not in the same genus;
in 1647 they will be in the same family, including the same genus;
in 13059 they will not be in the same family.

Therefore a random selected pair will be:

in the same genus once out of 83·1 selections;
in the same family once out of 8·93 selections;
not in the same family once out of 1·13 selections.

Table 3. *The number of genera with different numbers of species in each of the 32 habitats*

Habitat group	No. of species	No. of genera with 1 species	2 species	3 species	4 species	5 species	No. of genera
1 *a* 1	9	7	1	—	—	—	8
2	7	7	—	—	—	—	7
3	7	5	1	—	—	—	6
4	13	11	1	—	—	—	12
b 1	1	1	—	—	—	—	1
2	4	1	0	1	—	—	2
c 1	7	3	0	0	1	—	4
2	13	11	1	—	—	—	12
3	7	5	1	—	—	—	6
4	6	6	—	—	—	—	6
d 1	14	14	—	—	—	—	14
2	14	12	1	—	—	—	13
3	15	5	1	1	0	1	8
e 1	11	8	0	1	—	—	9
2	9	7	1	—	—	—	8
3	13	6	2	1	—	—	9
4	3	3	—	—	—	—	3
f	4	4	—	—	—	—	4
2 *a* 1	6	4	1	—	—	—	5
2	9	9	—	—	—	—	9
3	13	10	0	1	—	—	11
4	12	10	1	—	—	—	11
b	5	5	—	—	—	—	5
c 1	20	18	1	—	—	—	19
2	12	12	—	—	—	—	12
d	3	3	—	—	—	—	3
3 *a* 1	5	5	—	—	—	—	5
2	6	4	1	—	—	—	5
3	10	6	2	—	—	—	8
4	7	7	—	—	—	—	7
b	5	5	—	—	—	—	5
c	10	10	—	—	—	—	10
Total	280	224	16	5	1	1	247
Av. per habitat	8·75	7·00	0·50	0·16	0·03	0·03	7·72

Av. no. of species per genus per habitat = 1·132.

The numbers 83·1 and 8·93 are Simpson's measure of the Generic and Family Diversity.

It can easily be shown that:

for 3 species the chances that they will be congeneric are 233 out of 833,340 or 1 out of 3577;

for 4 species the chances they will be congeneric are 292 out of 35,208,615 or 1 out of 120,577;

and for 5 species, the chances that they will be congeneric are 1 in just over 3 million.

For an analysis of the frequency of genera with more than 1 species in a single habitat let us take as an example Moreau's habitat 1 *e* 3, which has 13 species in 9 genera, of which 2 genera have 2 species and 1 genus has 3. The 13 species contain $\frac{1}{2}(13 \times 12) = 78$ different pairs. Of these 2 pairs in the 2 genera with 2 species each, and 3 pairs in the genus with 3 species, are congeneric; i.e. a total of 5 out of 78 pairs are congeneric. We have, however, already seen that a random selection from the whole population only gives 1 congeneric pair in 83, so that this particular habitat has about five times as many congeneric pairs as would be expected by chance. For the same habitat the number of possible groups of 3 species is $(13 \times 12 \times 11)/(2 \times 3) = 286$; and the number of congeneric groups of 3 is 1 only, from the single genus containing 3 species. The expected frequency however (see above) is only 1 in 3577.

It is not desirable to argue from single cases, so Table 4 has been prepared to show similar analyses for each of the 32 habitats, for groups of 2, 3, 4 and 5 species, and giving at the bottom the total possible groups and the actual congeneric groups which are found in all the single habitats. The final results for the whole 32 habitats are as follows:

(1) Out of 1372 possible pairs of species selected at random within a habitat, 48 are congeneric. The number expected by random selection is $1372/83{\cdot}1 = 16{\cdot}5$.

(2) Out of 4829 possible groups of 3 species selected at random within a habitat, 19 are congeneric. The expected number by random selection is $4829/3577 = 1{\cdot}35$.

(3) Out of 13,427 possible groups of 4 species selected at random within a habitat, 6 are congeneric. The expected number is $13{,}427/120{,}577 = 0{\cdot}11$.

(4) Out of 30,713 possible groups of five species selected at random within a habitat 1 is a congeneric group. The expected number is 30,713/3 million = 0·01 of a genus.

Thus there are within the single habitat associations:

three times as many congeneric groups of 2 species,

fourteen times as many congeneric groups of 3 species,

fifty times as many congeneric groups of 4 species,

one hundred times as many congeneric groups of 5 species,

as would be expected in a similar set of species groups selected without reference to generic relations.

The same form of argument used above for species belonging to the same genus can be applied also to the relative frequency of species belonging to the same family. Out of the 14,706 ways of selecting 2 species at random there are 1647 pairs belonging to the same family. One would thus expect 1 random pair out of 8·93 to belong to the same family.

The total number of possible pairs within single habitats is 817 and the actual number of these pairs within the same family is 277. The expected number on random selection is 91·5. There are thus three times as many pairs of species of the same family within single habitats as would be expected by random selection from the total population of the whole area. Therefore not only has generic relationship some advantageous effect in determining the simultaneous survival of 2 species in a less complex animal association; but, in this particular set of data, the same also appears to be true of family relationship.

I have submitted the above analysis to Mr Moreau for his comments, and he replies that habitat 1 *d* 3 (lowland; semi-desert; riverine strips) was 'occupied during only that part of the year when food appears to be superabundant'. It is thus not so clear-cut as the others, and species may move in for feeding purposes only.

A high proportion of the congeneric species are found in this habitat. I am not sure that Moreau's statement makes it desirable to remove this habitat from consideration, as competition for food is one of the more definite types of interspecific competition. However, I have recalculated all the above figures relating to congeneric species, leaving out habitat 1 *d* 3.

In this habitat 7 species occur which are not mentioned in any other habitat. This reduces the total number of species in the area to 165 and reduces the size of several genera.

The following are the results:

I. *For pairs of species*

Whole fauna:

Total possible pairs 13,530

Congeneric pairs 153

Chance of a random pair being congeneric is 1 in 88·4

Single habitats:

Total possible pairs 1267

Congeneric pairs 33

or 1 congeneric pair in 38

This is 2·3 times as many as expected.

Table 4. *The number of species of birds in each of Moreau's 32 habitats—together with the number of different groups of 2, 3, 4 and 5 species which it is possible to select within each habitat, and the actual number of these groups that would be congeneric*

Habitat	No. of species	Pair of species		Three species		Four species		Five species	
		Possible	Congeneric	Possible	Congeneric	Possible	Congeneric	Possible	Congeneric
1 *a* 1	9	36	1	84	0	126	0	126	0
2	7	21	0	35	0	35	0	21	0
3	7	21	1	35	0	35	0	21	0
4	13	78	1	286	0	715	0	1,287	0
b 1	1	0	0	0	0	0	0	0	0
2	4	6	3	4	1	1	0	0	0
c 1	7	21	6	35	4	35	1	21	0
2	13	78	1	286	0	715	0	1,287	0
3	7	21	1	35	0	35	0	21	0
4	6	15	0	20	0	15	0	6	0
d 1	14	91	0	364	0	1,001	0	2,002	0
2	14	91	1	364	0	1,001	0	2,002	0
3	15	105	15	455	11	1,356	5	3,003	1
e 1	11	55	3	165	1	330	0	462	0
2	9	36	1	84	0	126	0	126	0
3	13	78	5	286	1	715	0	1,287	0
4	3	3	0	1	0	0	0	0	0
f	4	6	0	4	0	1	0	0	0
2 *a* 1	6	15	1	20	0	15	0	6	0
2	9	36	0	84	0	126	0	126	0
3	13	78	3	286	1	715	0	1,287	0
4	12	66	1	220	0	495	0	792	0
b	5	10	0	10	0	5	0	1	0
c 1	20	190	1	1,140	0	4,845	0	15,504	0
2	12	66	0	220	0	495	0	792	0
d	3	3	0	1	0	0	0	0	0
3 *a* 1	5	10	0	10	0	5	0	1	0
2	6	15	1	20	0	15	0	6	0
3	10	45	2	120	0	210	0	252	0
4	7	21	0	35	0	35	0	21	0
b	5	10	0	10	0	5	0	1	0
c	10	45	0	120	0	210	0	252	0
Total		1,372	48	4,829	19	13,427	6	30,713	1

II. *For groups of 3 species*

Whole fauna:
  Total possible threes 735,130
  Congeneric threes 165
    or 1 in 4460
Single habitats:
  Possible threes 4374
  Congeneric threes 8
    or 1 in 547
This is eight times the expected frequency.

III. *For groups for 4 species*

Whole fauna:
  Possible fours 29,772,765
  Congeneric fours 151
    or 1 in 197,171
Single habitats:
  Possible fours 12,071
  Congeneric fours 1
This is fifteen times the expected frequency.

Thus the effect of eliminating habitat 1 *d* 3 is to reduce the extent of the steady increase of observed over expected groups of congeneric species; but the same direction of increase remains, with no suggestion of any effect in the opposite direction.

DISCUSSION

It would appear from the above that when the bird populations of different ecological habitats, as defined by a competent field ornithologist, are studied, and when these habitats are sufficiently restricted so as to contain from 1 to 20 species with an average of less than 9, the statistical analysis of the relative numbers of species in different genera shows a definite excess of congeneric groups with 2 or more species above what would be expected by selection without reference to generic relations; and further that this excess seems to increase as the number of congeneric species increases.

When I brought forward somewhat similar evidence in 1947 for populations of insects and plants in the British Isles, the evidence was criticized by saying that the areas taken were too large and too complex, and within each there were many different habitats. While this is true of some of the areas previously considered, e.g. Wicken Fen or Windsor Forest—it is not true of some others—e.g. single plots on Park Grass Experimental Field at Rothamsted. But in any case the object was not to select absolutely simple environments (if, indeed, such things exist) but to select in pairs a more simple and a less simple area, the latter including the former, and to show that decreased ecological complexity was associated with decreased, and not with increased, generic diversity.

It appears to be established from the British evidence already discussed, and the above new evidence from East African birds, that within the limits of the evidence there are more congeneric groups in the simpler association than would be expected by random sampling from the larger fauna and flora of the surrounding area.

The average number of species in these bird associations is less than 9, and the number of expected pairs of congeneric species is only 1 in 83 pairs; so that it is not usually possible to demonstrate a difference from the expected in a single habitat. When, however, the results of all the 32 habitats are put together the result is overwhelmingly in support of less generic diversity in the simpler habitats.

If one accepts the usual view that closely related (congeneric) species compete so seriously with each other that it is not possible, or at least difficult, for them to co-exist in a single habitat, it is obvious that such habitats must be still smaller or simpler than those we have discussed, and with still fewer species,—in fact probably what are often called 'niches'.

It is also obvious, however, that the fewer the species there are in an association, the less chance there is of finding two congeneric species, even by chance and not by biological causes. How, then, is it possible to demonstrate that such competition is taking place. If a habitat contained say 4 species each in its own genus, and if (as is very probable) it could be shown that without any biological competition one would have expected such a result, how is it possible to demonstrate that there are more genera than would be expected? Only, it would seem, by having the 4 species in 5 genera!

The position at present is that down to the limits of about 9 species per habitat it is still possible to show that there is on an average an excess of congeneric species; that is to say too few genera—or a lower generic diversity than would be expected by random sampling. The upholders of the intra-generic competition theory believe that beyond this point there is a sudden reversal. But much beyond this point it does not appear to be possible to use the data of number of species and numbers of genera in small habitats to prove or disprove any continuation or reversal of the process of decreasing generic diversity.

What data then can be brought forward for analysis? Since up to the limits of present analysis there is no evidence of reversal it is surely the business of the supporters of the theory of intra-generic competition to produce evidence which supports it and shows statistically significant departures from the expected. I see at present no reason to alter my provisional explanation given in 1947, namely:

(1) That biological competition between closely related species is probably on an average greater than that between those less closely related.

(2) That closely related species are probably more suited to similar physical environments, and to similar extra-generic competition.

(3) That the balance of these two major factors, physical and biological, which determine the survival of species in different habitats, as shown by actual proportional survival in Nature, appears to indicate that the advantages of close relationship are on average greater than the drawbacks.

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REVIEWS

MOUNTAIN ECOLOGY

W. H. Pearsall (1950). *Mountains and moorlands.* Pp. xv and 312; 64 plates; 50 text-figures. New Naturalist Series. Collins, London and Glasgow. Price 21*s*.

For the ecologist this is perhaps the most useful volume yet published in the New Naturalist Series. In spite of Prof. Pearsall's fear, expressed in the preface, that the book might be thought 'remarkable more for its omissions than its scope', most readers will be more than satisfied with the information contained in it, and will find most of the problems which they have met with in upland ecology either discussed or referred to. In this one volume the author has recorded his own observations and conclusions reached after over thirty years' work in the hills, and synthesized these with other relevant work, much of which has hitherto been scattered in journals.

The present vegetation is shown vividly to be in a constant state of flux and to have developed as a result of the complex interaction of topography, rock, climates, glaciation, soil and man's activities. The perplexing variety of upland vegetation becomes intelligible as different stages in a developmental series, either natural or induced by man. The book is not easy reading, nor is it intended as such; the serious worker will read it several times and constantly refer to it. Students of zoology, botany and geography are already being told 'there is a good discussion of that in Pearsall's book', often about some subject to which no easy reference could formerly be given.

After an Introduction there are chapters on Structure and Climate. The geological basis for our mountains and their scenery is described, with a useful account of glaciation and of physical instability as a typical feature of uplands. The climate is compared to that of the lowlands, and the rainfall requirements for bog formation and leaching are discussed and the effect of altitude on animals and plants. Altitudinal zonation is largely controlled by temperature which is illustrated by the interesting example of *Juncus squarrosus* and the rush-moth *Coleophora caespititiella*.

Chapter 4 deals with Soils, and describes the varied stages of soil formation and the trends of development: skeletal and immature soils of the mountain summits and scree slopes, flushed and leached soils, waterlogged soils and peat. When upland surfaces become stable enough to permit complete vegetation cover they inevitably tend to become leached, and owing to the high summer rainfall this process can never be completely stayed. Impermeable pan layers form, which impede drainage and ultimately lead to peat formation. The biological characters of soils are discussed and the effects of waterlogging, leaching and low temperatures are shown to be similar in reducing the activity of the aerobic soil population and so producing peat or peaty humus.

Chapter 5 describes the Mountain or montane vegetation, usually found at altitudes of 2000 ft. and upwards, and this is subdivided into colonizing communities, montane grasslands, vegetation on leached soils (summit heaths) and flush vegetation. The first three of these represent the normal trend of development on mountain top detritus with increasing stability of surface. While most of the vegetation on a British mountain consists of montane grassland, often dull and poor in plant species because of grazing, the special montane plants, which are rarely found at low altitudes, are of great interest. The chapter concludes with a good discussion of the habitat requirements of these special plants, which are the remains of a vanishing flora.

The next three chapters are concerned with the submontane vegetation. In chapter 6 (Grasslands) sections are devoted to *Festuca-Agrostis* grassland, bracken, *Nardus*, *Molinia*, grass heaths and flushed pastures. The nutritive value and palatability to stock of these grassland types are compared, and the biological effects of overgrazing are described. It is confusing to have *Deschampsia flexuosa* described in different places as Wavy Hair Grass and Silver Hair Grass, and *Molinia* as Moor Grass and Blue Moor Grass. All the existing submontane grasslands have probably been derived from woodland, and the remaining fragments of these are dealt with in chapter 7, with their associated floras. The six main categories are the mixed woods on unstable and flushed soils, oak, alder, birch, pine and the new state forests. Wood degeneration and its causes are discussed and the former distribution of woods as shown by place names and buried timber. The next chapter on Moorlands and Bogs describes first the moors of drier type, bilberry and heather moors, and then the wet bogs. Useful lists of plants are given to show the average composition of a heather moor and of three widely separated bogs. Mixed moors of heather and cotton-sedge are the most extensive type in Britain to-day, while in the South Pennines there are large areas of cotton-sedge moor. The author gives evidence to show that most present-day moorland vegetation on deep peat, including the cotton-sedge moor, has been derived from bog, through the agencies of grazing, burning and draining.

Having dealt with the upland vegetation in detail, there now follow two chapters dealing with its relationship to habitat and to ecological history. To illustrate the latter two sample areas, the Lake District and Ringinglow Bog, are described and the evidence from lake bottom sediments and from peat respectively are correlated with the human history of the areas. These examples show impressively how large vegetational differences in the uplands can be due to varying intensity of man's occupation and exploitation.

In the next three chapters the upland animals are discussed. Chapter 11, The Invertebrates, shows first how little is known about the ecology of these animals, and also how difficult it is to give a general account of them because the species are many and hard to identify. However the author shows clearly how the fauna is

dependent on soil, vegetation and climate, and this chapter is full of information which it would be hard to find elsewhere. The beetles and moths are described in some detail, as there is more information about them, and the study of a heather moor which is being carried out by the Yorkshire Naturalists Union. The chapter on Large Mammals and Birds gives a list of species breeding or resident above 1000 ft., and then discusses their significance. The original fauna of the moorlands can be visualized from the records of trapping of the early nineteenth century, and the widespread destruction of the predators since that time, due to game preservation, has had important influence on the natural animal groupings. There is a possibility of certain 'dispossessed' species returning to their old localities if the state forests are organized for constant regeneration.

To-day the three most distinct animal groupings in the uplands are grouse moor, deer forest and sheep-walk, and the development of these man-made communities is traced in chapter 13, by examining the archaeological and historical evidence. The turning of much of the land into sheep-walk has taken place at different times in different parts of Britain, mainly according to accessibility, with a predominant part played by the Cistercian Abbeys and their wool trade in the north.

In the final chapter on the future, Prof. Pearsall wisely points out that conservation and utilization of the uplands are not so incompatible as might appear. Blind conservation is not possible where changes of soil and vegetation are taking place, and control can equally well be directed towards regeneration of what is fast disappearing, such as good pasture and forests. The relative merits of grazing and afforestation for the utilization of the uplands are discussed, but the basis for either should be the improvement of the soil fertility.

The thirty-two colour plates are the one disappointing feature of this book, as of other New Naturalist volumes. At first sight they may appear to be attractive, like many of the posters advertising holiday resorts, but actually the colours as reproduced are often false and exaggerated, though the original transparencies are probably first class. Lakes are too blue, distant hills too purple, yellows and browns too bright in many cases, and those who live in the hills know and prefer the softer and more subdued colours, which are more typical of their climate. The close-up colour photographs of animals and plants suffer less from this colour distortion but they too are variable; thus in plate 15 surely the predominant brown of the Liverwort flush should not extend to the leaves of the Golden Saxifrage.

The same number of plates in black and white, on the other hand, are good and they include seven fine aerial photographs. Many people would probably prefer a higher proportion of black and white plates in these volumes, until a better technique of colour reproduction can be evolved. Of great value to the reader of this volume are the 50 text-figures, many of which are field sketches and field diagrams.

All naturalists, to whom this book is dedicated, will be grateful to Prof. Pearsall for this scholarly account of the ecology of the British Uplands.

P. F. HOLMES

MAN AND MOSQUITOES

H. S. Leeson, W. H. R. Lumsden, J. Yofe & T. T. Macan (1950). *Anopheles and malaria in the Near East.* Pp. xii and 223; 73 text-figures. London School of Hygiene and Tropical Medicine, Memoir No. 7, H. K. Lewis, London.

In this memoir are published a short introduction by Prof. P. A. Buxton and three papers: 'Anopheline surveys in Syria and Lebanon', by Major H. S. Leeson, R.A.M.C.; 'Anophelism and malaria in Transjordania and in the neighbouring parts of Palestine and Syria', by Lieut.-Col. W. H. R. Lumsden, R.A.M.C., and Lieut.-Col. J. Yofe, R.A.M.C., and 'The Anopheline mosquitoes of Irak and North Persia', by Major T. T. Macan, R.A.M.C. All three papers relate to investigations during the last war by Field Malaria Units engaged in the survey and control of malaria in the countries mentioned. All contain much that will be of interest not only, as the title might suggest, to those concerned with malaria and its control, but for the student of zoogeographical distribution and, among others, for the ecologist. It is in this last context, as a study of anopheline faunas and of the ecological factors influencing their constituent species that the present review is especially concerned. It will be most informative to take seriatim the findings of these papers in the order they have been presented.

After a description of the physiographical, climatic and other relevant features of the area in Syria and Lebanon surveyed by No. 2 Malaria Field Laboratory, Major Leeson records the methods used in the survey, the species of anopheles encountered and the types of breeding place in which they were found with information on seasonal occurrence and other data. A feature of the paper are some excellent photographs showing characteristic examples of terrain and of breeding places. On the west, bordering the Mediterranean, is a strip of country about 10 miles wide in which everywhere *Anopheles saccharovi* breeds in coastal swamps. Inland from this are the coastal mountains rising to 9000 ft., pre-eminently the abode of *A. superpictus*. Still farther east is the central plain where throughout the entire area *A. saccharovi* is the main vector of malaria and *A. superpictus* plays a minor role. Then follow the inland mountains with *A. superpictus* the dominant species and *A. saccharovi* occuring sporadically in swamps and some heavily irrigated areas. Finally, beyond this, lies the inland desert extending eastwards to the borders of Irak. In the desert there are large springs from which rivers originate. Water is raised from these by uplift forming swamps in all of which *A. saccharovi* breeds. *A. saccharovi* is the form referred to in the earlier literature as *A. elutus*, a near relative or subspecies of *A. maculipennis* the common European anopheles. It was noted in Europe for frequenting coastal and brackish waters and for its potency as a vector of malaria. *A. maculipennis* in its typical form the author notes was not encountered in the area. Other species recorded were: *A. claviger*, *A. sergenti*, *A. algeriensis*, *A. hyrcanus*, *A. multicolor*, *A. marteri* and *A. pulcherrimus*. The last-mentioned species was found only once and that in north-east

Syria (Upper Euphrates). *A. claviger* (*A. bifurcatus* of older records) had a patchy distribution, being found in some villages and not in others, though it was nearly always found near the large towns. Its breeding places were wells, tanks and cisterns. In the adult form it was found occupying especially cool and dark places. *A. sergenti* was taken as far north as just south of Tartus (35° N.). The species has been recorded from many localities in Palestine. *A. algeriensis* is commonly a spring species occurring especially in winter-formed swamps. In the present survey it was found along with other species in the coastal strip swamps and irrigation channels. *A. marteri* is a hill species at first known only from Algeria, but later found to have a wide distribution in the mountain streams of south European countries. *A. hyrcanus* was not very common. *A. multicolor* was taken only once from south of Tyre. It is *par excellence* a desert and saline breeding species with a Saharan distribution. All the species mentioned, with the exception of *A. claviger* and *A. pulcherrimus*, have wide distributions from the west across North Africa or South Europe to Palestine and beyond.

Lumsden and Yofe, in their paper, describe the physiographical features and the anophelines associated with these in Transjordania and neighbouring areas. Forming the western boundary is the Ghor, or Rift Valley, 600–1000 ft. below sea-level in which lie the Dead Sea and the Jordan valley. East of this is the escarpment of the western highlands intercepting much rainfall and deeply dissected by torrents. Then follows the plateau, a long gradual slope extending to the borders of Irak. Eleven species of anopheles were recorded, those most frequently encountered and most likely to be concerned in malaria transmission being *A. saccharovi*, *A. superpictus* and *A. sergenti*. The first is limited in its distribution to the north of the plateau and the Ghor. The other two are practically co-existent with the surface water. *A. superpictus* and *A. sergenti* largely use the same type of breeding place, but are complementary rather than competing. *A. superpictus* inclines to more sunlit waters, whilst *A. sergenti* prefers those partly shaded. Further the two species pass the winter in entirely different ways, *A. superpictus* as adults with gonadal diapause and fat body development (hibernation), *A. sergenti* in the larval stage (overwintering by larva). In spring, *A. superpictus* can rapidly attain a high larval density as soon as diapause ends. *A. sergenti* must await the hatching of adults from overwintering larvae. Other species recorded are: *A. claviger*, *A. algeriensis*, *A. marteri*, *A. hyrcanus*, *A. dthali*, *A. hispaniola*, *A. multicolor* and *A. rupicolus* Lewis. The species are substantially as recorded by Leeson for Syria and still represent the same general faunal complex. *A. pulcherrimus* was not encountered. *A. dthali* occurred only in six collections. This is a species with an Arabian and north-east African distribution. *A. rupicolus* was found in one locality only. Previous records are the Sudan and Sinai. *A. hispaniola* was found on three occasions. It is typically Mediterranean, having been taken as far west as the Canary Islands and Spain.

The paper by Major Macan dealing with the anopheline mosquitoes of Irak and North Persia contains a wealth of information regarding these countries and their anopheline fauna. Especially regarding north Persia the information given is entirely new and extremely valuable. Perhaps the most outstanding physical feature of the area is the alluvial plain of the Tigris and Euphrates. This is a vast delta built up by the rivers. At its upper end it is largely dry desert, in its lower parts there are extensive reedy lakes and marshes. Here *A. pulcherrimus* is the dominant species. It occurs sometimes in vast numbers but fortunately appears to play little or no part in malaria transmission. The important vector species is *A. stephensi*, though *A. saccharovi* has to be considered over a small part of the Shatt-al-Arab area. *A. stephensi* flourishes in the date palm gardens of the lower Shatt-al-Arab where inundation irrigation is practised. Otherwise, as in India, the species occurs in small collections of water nearly always of man's creating. There is reason to believe that since 1919, when its distribution was mapped by the present writer and Shortt, the species has spread northwards through the alluvial plain with associated malaria well up the Euphrates and to Baghdad and beyond. To the east of the alluvial plain is an area of foothills and beyond this the escarpment of the Zagros mountains edging the Persian plateau. Here *A. saccharovi* and *A. superpictus* are the dominant species. The latter was abundant throughout the foothills and escarpment and also beyond on the Persian plateau. *A. saccharovi* was recorded at 148 different places. Other species encountered were: *A. claviger*, *A. marteri*, *A. algeriensis*, *A. hyrcanus*, *A. multicolor*, *A. fluviatilis*, *A. culicifacies*, *A. turkhudi*, *A. arabica*, *A. sogdianus*, *A. dthali* and *A. maculipennis* type form. Of these a number have already been recorded in the two previous surveys and are mainly species representing the same Mediterranean fauna as in the areas there studied. *A. marteri* was found by Major Watson in the upper portions of most, if not all, the mountain streams in the escarpment region. *A. algeriensis* was taken in eighteen places from streams or swamps in the foothill and escarpment region chiefly in the spring. *A. multicolor* was taken in five places, as usual in saline water. *A. dthali* had a widespread distribution occurring especially in the Karun and southern foothill area. But besides these species are others whose faunal relations are with the Oriental faunal realm. Two such, viz. *A. pulcherrimus* and *A. stephensi* have already been mentioned, but in addition are *A. fluviatilis*, *A. culicifacies*, *A. turkhudi* and *A. arabica*. Whilst the first two may be said to have occupied the alluvial plain, or to be in process of doing so, the others for the most part have been recorded only towards the Persian Gulf. *A. fluviatilis*, however, was taken in a number of places in the escarpment area and in one locality on the Arabian plateau to the west.

Of special interest are the author's observations regarding the last-mentioned species, *A. maculipennis*. Records of this form are noticeably absent from the two previous surveys, and the same applies to all records in the present survey except those to the north-east on the escarpment or Persian plateau beyond. Here the species was taken in seventy-three different places by No. 1 and from thirty-nine places by No. 10 Malaria Field Laboratory. Its appearance clearly indicated evidence

of a still further faunal region, viz. the typical palaearctic as contrasted with the Mediterranian facies with which we have been so far mainly dealing or, as given in the author's adoption of divisions of the palaearctic region, Euro-Siberian. Both *A. maculipennis* and *A. saccharovi*, the author notes, are found in the same sort of breeding place, but are seldom found together. A slight change in environment would appear to favour one to the disadvantage and often complete disappearance of the other. It was thought that available data pointed to maximum temperature as the factor limiting the range of *A. maculipennis*. The distribution of the species recorded is very clearly shown in maps in the text, and the paper is illustrated with some very interesting photographs of types of country and of breeding places.

The memoir in itself is most attractively produced and in its contents and careful editing and presentation is a worthy successor of previous memoirs of the series, the publication of which we are glad to see, from Prof. Buxton's introduction, is to be resumed.

S. R. CHRISTOPHERS

ANIMAL DISTRIBUTION

L. F. de Beaufort (1951). *Zoogeography of the land and inland waters.* Pp. viii and 208; 10 text-figures. Textbooks of Animal Biology. Sidgwick and Jackson, London. Price 30*s*.

The 184 pages of text are divided into nine chapters: Introduction; Holarctic Region; British Isles; Oriental Region; Ethiopian Region; Madagascar and the neighbouring islands; Neogaea; Notogaea; Celebes, Moluccas, and Lesser Sunda Islands. Neogaea is the South American region, Notogaea Australia, New Zealand, and neighbouring islands.

In the introduction the author points out that the area occupied by any species to-day depends on three factors: past history, the range of environmental conditions that it can tolerate, and its powers of getting from place to place. He dwells briefly on the species problem. Some readers will be disappointed that only the first of these four themes is developed further. Some animals have recently been transported by man across boundaries previously impassable. Their subsequent history has been varied; some have spread with astonishing rapidity, others have done no more than establish and maintain themselves at the point of introduction. Much has been written about this subject, and a summary would help us to understand what happened in the past when land bridges came into existence, and correct the widespread impression that a sample of animals moving down a land bridge was comparable to a sample mounting the gangway of Noah's ark. The ecologist will take criticism further than this and ask why, for example, the vexed question of the Lusitanian fauna is discussed without any reference to the peculiar climatic conditions under which the species live to-day.

All the chapters conform closely to a common pattern, and chapter 4, on the Ethiopian Region, may be taken as an example. The first paragraph describes the boundaries, stressing that hard and fast lines cannot be drawn where the boundaries cross land. The second paragraph describes the climate. Similarities between the forest fauna of Africa and India are mentioned, four pairs of closely related genera and one common genus of mammals, and three families of birds being named. From the Miocene to the Pliocene forest stretched uninterruptedly from Africa to India. None the less, there are big differences, notably the absence of deer and bears from the Ethiopian Region, and these are difficult to explain. The advent of drier conditions not only separated India and Africa, but divided Africa into separate forest regions; the resulting isolation has led to species formation in some instances, and four mammals are quoted as examples of this.

On the fourth page of the chapter the account passes to the animals of open country. The Hyracoidea are confined to Africa, Palestine, Syria, and Arabia, but were once more widespread, as the fossil record shows. The giraffes, antelopes, zebras, elephants and ostriches are thought, on fossil evidence, to have originated in the Holarctic Region. The fossil record is not fully discussed. Knowing how difficult it is to show convincingly that a species is absent from any area to-day, I should like to have read more about the fossiliferous deposits in Africa and what was found in them at a time when the animals under discussion were known from further north. All we learn, however, is that (p. 96) 'Matthew has strongly urged the view that all the mammalian orders originated in the northern continents', and that (p. 95) 'The fossil mammals of Africa are not nearly so well known as those of the northern continents.' The elephants, aardvarks, and hippopotamuses are discussed, but nothing certain can be said about their origins. Three families and one genus of Insectivora are mentioned. All are peculiar to the region, but nothing is known about their past history.

Pluvial periods in Africa probably coincided with glacial periods in the Holarctic. They influenced the fauna. A page and a half and a map are devoted to certain birds which illustrate this point. Occupying most of Africa in a dry period, the species were isolated into groups by the advance of forest during a wet period. Subspecies developed and these, having advanced as the forest retreated with the onset of drier conditions, now overlap in some areas, and where they meet they interbreed.

The remaining eight pages are devoted almost exclusively to fish. In the preliminary account there are three species, sixteen genus, and fifteen family names. The work of Worthington on the fishes of the African Lakes is then described. On the penultimate page reference is made to the peculiar fauna of Lake Tanganyika, and invertebrates are mentioned for the first time; ten genera of Molluscs with a wide tropical distribution and ten endemic to the lake are listed.

In some of the other chapters the reader is left with the wish that there had been at the beginning some consecutive account with maps of the geographical changes that have been important in animal distribution. Thus in the chapter on the Holarctic Region he learns on p. 27 that the Alps projected from the sea as a peninsula of eastern Europe and Asia in Tertiary times; on p. 39 that the Sarmatian Sea covered Hungary, the

northern part of the Balkans, the Black Sea, and the Caspian Sea; on p. 40 that in early Tertiary times the Sarmatian Sea had connexion with the Bay of Bengal; and on p. 43 that, in the Miocene, Spain was cut in two by a channel connecting the Atlantic and the Mediterranean. The resulting picture of Europe and Asia in this reader's mind is not a clear one. The chapters on the Holarctic and the British Isles contain no reference to Thienemann's recent volume in *Die Binnengewässer* on the history of the European fresh-water fauna. Presumably the two books have been written at the same time, neither author knowing what the other was doing. This coincidence is much to be regretted. To take up a point of detail, the statement on p. 26 that the present distribution of *Planaria alpina* is not due to the Ice Age is likely to set the cat among the pigeons. The statement is based on a paper which, being in Dutch, is likely to remain unknown to most workers. As there is no other reference at all, it is perhaps invidious to complain that the author, like all continental writers, has ignored the work of R. S. A. Beauchamp.

This book is one of a series, and it is clear that Prof. de Beaufort has been asked to cover a very wide field in a small compass. It is unfair to overlook this in a review; what the reader would like to have read, and what the author would like to have written had space permitted may well be identical. Within the limits set de Beaufort has packed a great deal of information, presented in concise English that no-one would suspect was not written by a native of this country.

There are ten text-figures, all but one maps. One hundred and thirty two works are referred to in the bibliography. The index is 16 pages long. The print is large. Only a few small errors were noticed: 'dessication' on p. 11 is spelt correctly on p. 106; Trewawas on p. 105 should be Trewavas; and Japen on p. 158 I take to be a slip for Japan.

T. T. MACAN

THE FINANCING OF RESEARCH

Sixth annual report of the Nuffield Foundation (1951). Oxford.

This report, which covers the year ended 31 March 1951 opens with s apirited and extremely well-written defence of the principle of private charity, accompanied by a powerful attack on the idea that because a statutory authority has power to operate in any particular field it is therefore unnecessary or undesirable for independent bodies to interest themselves in it. Accounts are given of the many research projects to which the Foundation is giving support, especially, for the current quinquennium, in the fields of Biology and Social Science. It is interesting to note that one of the larger new grants is to the Zoology Department at Oxford in aid of the work of Dr E. B. Ford, F.R.S., on physiological genetics and the evolutionary genetics of wild populations. Much of the sociological research which is being supported at various universities and elsewhere is also essentially ecological in outlook.

BOOKS RECEIVED

Island of Skomer. A preliminary survey of the Natural History of Skomer Island, Pembrokeshire, undertaken for the West Wales Field Society. Edited by JOHN BUXTON and R. M. LOCKLEY. Staples Press, London. 1951. Price 18*s*.

Animal evolution. A study of recent views of its causes. By G. S. CARTER. Sidgwick and Jackson, London. 1951. Price 30*s*.

A natural history of man in Britain. By H. J. FLEURE, F.R.S. The New Naturalist Series, Collins, London. 1951. Price 21*s*.

Beans. Ministry of Agriculture and Fisheries, bulletin no. 87. Published 1935, new edition 1950. H.M.S.O. Price 2*s*.

Poultry breeding. Genetics and systems of breeding. By G. E. MANN. Ministry of Agriculture and Fisheries, bulletin no. 146. H.M.S.O. 1951. Price 3*s*.

The wood pigeon in Britain. By M. K. COLQUHOUN. Agricultural Research Council Report Series, no. 10. H.M.S.O. 1951. Price 3*s*.

Evolution in outline. By T. NEVILLE GEORGE. Thrift Books, no. 1.

What's all this about genetics? By RONA HURST. Thrift Books, no. 3.

The ladder of life. By A. GOWANS WHYTE. Thrift Books, no. 4. Watts, London. 1951. Price 1*s*. each.

Ecology of animal parasites. By JEAN G. BAER. University of Illinois Press. 1951. Price $5.00.

Audubon water-bird guide. By RICHARD H. POUGH. Doubleday, New York. 1951. Price $3.50.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Several papers omitted in the last few years are being noticed in this and following issues. Papers in the *Journal of Animal Ecology* itself are not dealt with. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, The Ferry House, Ambleside, Westmorland.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by R. Bainbridge, H. F. Barnes, G. I. Crawford, A. E. Ellis, R. S. R. Fitter, I. M. Goodbody, L. A. Harvey, A. Macfadyen, C. Matheson, E. Nelmes, E. R. Parrinder, and Miss G. Watt; checking by B. M. Hobby; abstracting and editing by R. S. R. Fitter.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	260
(*a*) Marine and brackish	260
(*b*) Fresh water	261
(*c*) Land	261
(*d*) Small islands	263
2. General reports and taxonomic studies of use to ecologists	263
3. Parasites	264
4. Food and food habits	264
5. Population studies	266
6. Migration, dispersal and introductions	267
7. Reports of organizations	269

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Foster, J. & Gibb, J. (1950). 'Shore feeding ecology.' Bird Notes, 24: 83–6.

A demonstration of Gause's principle that no two birds having identical ecology can live side by side in the same habitat in relation to birds feeding on the shore of a Scottish sea loch in August 1949.

Gotto, R. V. (1951). 'Some plankton records from Strangford Lough, Co. Down.' Irish Nat. J., 10: 162–4.

A list of species taken in surface hauls between November 1947 and March 1949, with data on seasonal abundance for some of them. The Strangford plankton fauna seems to agree more nearly with that of Port Erin (40 miles south-east) than with Millport (100 miles north-north-east).

Quick, H. E. (1950). 'Observations on *Limapontia*.' Proc. Malac. Soc. Lond. 28: 134–8.

Additional records of *Limapontia depressa* in Britain on saltmarshes bordering muddy estuaries; and of *L. capitata*.

(*b*) Fresh water

Alley, R. & Boyd, H. (1949). 'Effects of the cold spell of 1947 on the coot in north Somerset.' Brit. Birds, 42: 225–32.

Mortality varied from one water to another, and factors causing this are discussed, the availability of food being considered the most important.

Hickin, N. E. (1950). 'Larvae of the British Trichoptera. 30.' Proc. R. Ent. Soc. Lond. 25: 103–6.

The larva of the Psychomyid *Tinodes pallidula*, here described and figured, inhabits a tunnel made of sand grains with mud, algal filaments, and occasional small pebbles cemented together with a silk-like secretion.

Hickin, N. E. (1950). 'Larvae of the British Trichoptera. 31.' Proc. R. Ent. Soc. Lond. 25: 107–10.

The larvae of the Limnophilid *Stenophylax vibex*, here described and illustrated, frequented a small stream some 2 to 4 ft. in width with a stony bottom alternating with patches of clay. They construct cases of peat-like fragments of vegetable debris.

Höhn, E. O. (1949). 'Notes on sexual and territorial behaviour in the coot and on the incidence of non-breeding in this species.' Brit. Birds, 42: 209–10.

Two examples of populations of about 50 *Fulica atra* with neither nests nor young in June and July. Some instances of frogs (*Rana temporaria*) in the diet are given.

(*c*) Land

Andrews, H. W. (1950). 'Notes on some Diptera at St David's, Pembrokeshire.' Ent. Rec. 62: 18–21.

A list, sometimes with habitats, localities and numbers, of Dolichopodids, Syrphids, Tachinids, Anthomyiids, and a few flies of eight other families that were collected during late May and early June 1949. It is stated to be only partially representative of the local dipterous fauna. Topographical notes are included.

Ash, J. (1949). 'Roosting behaviour of chaffinches.' Brit. Birds, 42: 289.

Barker, J. F. (1949). 'Roosting habits of dipper.' Brit. Birds, 42: 389.

Roosts are usually under waterfalls, in hollows in the stonework.

Bedford School Natural History Society (1950). Observations on a Bedfordshire rook roost. Bedfordshire Nat. 4: 31–6.

Observation on a roost used by rooks and jackdaws during 1949.

Blair, C. A. (1950). 'Observations on the life history of the fruit tree red spider *Metatetranychus ulmi* (Koch).' Rep. E. Malling Res. Sta. 1949 (37): 143–5.

Biology. Numbers reduced by predatory Capsid *Blepharidopterus angulatus*. Wild hosts: *Prunus spinosa*, *Crataegus oxycantha*, *Rosa canina*, *Pyrus malus*, *Ulmus* spp. and *Salix* spp. In gardens also *Ribes sanguineum* and *Cotoneaster* spp.

D., F. H. (1950). 'The leaf-nest aphis *Prociphilus nidificus* (Lw.) on ash in North Wales.' Quart. J. For. 44: 223–4.

Two infected trees in Caernarvonshire represent a considerable extension of range for an aphid that is at present only known from Scotland, but is probably more widely distributed in the British Isles.

Davies, J. L. (1949). 'The breeding status of the starling in west Wales.' Brit. Birds, 42: 369–75.

Sturnus vulgaris is a local and rather scarce breeder in west Wales, being confined to towns and large villages below 500 ft., and has still not colonized large areas which appear quite suited to it. The weather is suggested as the only factor which could account for this.

Dicker, G. H. L. (1950). 'The strawberry aphid, *Pentatrichopus fragaefolii* (Cock.), and its control.' Rep. E. Malling Res. Sta. 1949 (37): 132–8.

Life history, with emphasis on the dispersal period in May and June.

Dicker, G. H. L. (1950). 'The shallot aphid, *Myzus ascalonicus* Doncaster, a pest of cultivated strawberries.' Rep. E. Malling Res. Sta. 1949 (37): 139–40.

Life history, with special reference to the cultivated strawberry.

Gillham, E. H. (1949). 'Corn-bunting roosts in the north Kent marshes.' Brit. Birds, 42: 328.

Roosts in reed-beds.

Goodey, J. B. (1951). 'The potato tuber nematode, *Ditylenchus destructor* Thorne, 1945; the cause of eelworm disease in bulbous iris.' Ann. Appl. Biol. 38: 79–90.

Cross-inoculation experiments showed that the eelworm causing disease in potato tubers would set up characteristic symptoms in iris bulbs and vice versa. Transfers were also made from potato and iris to *Mentha arvensis* and from iris to *Sonchus arvensis*. Biology of *Ditylenchus destructor* is compared with that of *D. dipsaci*.

Guild, W. J. McL. (1951). 'Earthworms in agriculture.' Scot. Agric. 30: 220–3.

The weight of worms below the surface of a pasture field is not much less than the weight of stock which the field would carry. An average figure is 250,000 active worms weighing 4–6 cwt. and casting 10–15 tons of soil per year or one inch every 6–10 years. Populations on arable land are much less. Bimodal curve of activity with peaks in the spring and autumn.

Hayman, R. W. (1949). 'Nesting sites and local concentration of kestrels.' Brit. Birds, 42: 90.

Six nests in holes on trees within a radius of five-eighths of a mile.

Hincks, W. D., Ainsworth, G. H. & Butler, P. M. (1951). 'The entomology of Spurn Peninsula.' Naturalist: 75–86.

The first part of an ecological survey dealing largely with the insect fauna of Spurn. Contains a short introduction to the ecology of the area, including the main plants, notes on the general zoology and detailed treatment of the entomology of the marram grass areas.

Johnson, R. H. (1951). 'An investigation into the animals to be found on a tree stump and a comparative estimation of their numbers.' Rep. Rugby School Nat. Hist. Soc., 84: 14–17.

An investigation on a 4-year-old tree-stump during February-March 1950. Woodlice were the commonest animals, followed by spiders, centipedes and millipedes.

Kennedy, J. S., Ibbotson, A. & Booth, C. O. (1950). 'The distribution of aphid infestation in relation to leaf age. I. *Myzus persicae* (Sulz.) and *Aphis fabae* Scop. on spindle trees and sugar-beet plants.' Ann. Appl. Biol. 37: 651–79.

Growing and ageing leaves were more susceptible to colonization than maturing, mature and dying leaves. When both aphids were infesting the same plant at the same time, *M. persicae* extended on to both younger and older leaves than did *A. fabae*. It is suggested that the degree of adaptation of a given aphid to a given plant may be gauged by the extent to which the aphid can colonize the plant's leaves not only when they are growing and ageing but also when they are mature and fully functional.

Lucas, C. M. (1950). 'Slugs in a Bedford garden.' Bedfordshire Nat. 4: 50.

Regular samplings once a month showed that *Agriolimax reticulatus* was by a very large margin the dominant species. Six other species were present.

Manser, G. E. & Owen, D. F. (1949). 'Spring roost of yellow wagtails.' Brit. Birds, 42: 244.

In a reed-bed.

Massee, A. M. (1950). 'Notes on some interesting insects observed in 1949.' Rep. E. Malling Res. Sta. 1949 (37): 126–31.

Includes pear sawfly (*Hoplocampa brevis*) outbreak in Kent (only previous record in England was in 1934 at Cambridge) and notes on the predaceous mites found on fruit in this country.

Oakes, C. (1949). 'Status of green woodpecker in Lancashire.' Brit. Birds, 42: 186–7.

A recent increase in both *Picus viridis* and *Dryobates major* in Lancashire may be correlated with the widespread felling of timber in other parts of the north of England.

Owen, D. F. & Owen, J. E. (1950). 'The butterflies of Greenwich Park.' Ent. Rec. 62: 15–6.

Notes, based on daily observations during 1944–7, on the status, abundance and habitats of 23 species, with topographical details. *Maniola tithonus*, *Nymphalis polychloros* and *Callophrys rubi* have become extinct or virtually so since 1902, *Anthocaris cardamines* and *Nymphalis io* no longer breed, *Polyommatus icarus*, *Thymelicus sylvestris* and *T. lineola* are decreasing, and *Polygonia c-album* is increasing. *Thymelicus sylvestris*, *T. lineola* and *Ochlodes venata* were not listed in this area in 1902. The decrease in the number of breeding species is attributed to urbanization of the surrounding area.

Owen, J. E. (1950). 'The Rhopalocera of the Darent Valley between Shoreham and Eynsford, Kent.' Ent. Rec. 62: 73–5.

Notes on the present-day status of 42 species. The butterflies *Pararge aegeria* and *Limenitis camilla* have recently become established, and only *Hesperia comma* is decreasing.

Pitcher, R. S. (1950). 'Slug damage to raspberry canes.' Rep. E. Malling Res. Sta. 1949 (37): 131.

Agriolimax reticulatus feeding on young canes in May and early June.

Robinson, W. (1950). 'Montagu's harriers (*Circus pycargus*).' Bird Notes, 24: 103–14.

Includes sections on habitat, nest site and food.

Soper, F. G. R. (1950). 'Woodpeckers—before and after the great frost.' Bedfordshire Nat. 4: 51.

In a Bedford garden *Dryobates major* completely supplanted *Picus viridis* after the frost of 1947.

Woodroffe, G. E. (1951). 'A life-history study of the brown house moth, *Hofmannophila pseudospretella* (Staint.) (Lep., Oecophoridae).' Bull. Ent. Res. 41: 529–53.

Only important predator was the mite *Cheyletus eruditus* which destroyed numbers of eggs and young larvae.

(*d*) Small islands

Conder, P. J. (1951). 'The factors affecting the distribution of wheatears on Skokholm.' Rep. Skokholm Bird Obs. for 1950: 15–19.

Rabbits are the most important factor controlling the distribution of *Oenanthe oenanthe* on this Pembrokeshire island. They graze the vegetation down to a suitable height and provide, directly or indirectly, many of the nesting holes.

Harvey, L. A. (1951). 'The granite shores of Lundy.' Ann. Rep. Lundy Field Soc. for 1950: 34–40.

A preliminary account of the flora and fauna of the shores of this island in the Bristol Channel.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Broadhead, E. (1950). 'A revision of the genus *Liposcelis* Motschulsky with notes on the position of this genus in the order Corrodentia and on the variability of ten *Liposcelis* species.' Trans. R. Ent. Soc. Lond. 101: 335–88.

A taxonomic revision of the 22 species of this genus and a comparison of the variability of the parthenogenetic *Liposcelis bostrychophilus* with those of nine bisexual species and a comparison of the variability of the two sexes in nine species.

Hosking, E. (1949). 'Bird photography by high-speed electronic flash.' Brit. Birds, 42: 240–1.

A brief description of the technique, accompanied by 24 photographs.

Hosking, E. & Smith, S. (1949). 'High-speed photography as an aid to the identification of prey.' Brit. Birds, 42: 258.

Both insect and small mammal prey can be identified readily from high-speed flash photographs.

Scott, P. (1951). 'The swans, geese and ducks of the British Isles.' Ann. Rep. Severn Wildfowl Trust, 3: 121–30.

Brief notes on British swans and geese, accompanied by excellent illustrations in colour. It is considered that the blue goose (*Anser caerulescens caerulescens*) may be an occasional wild visitor to the British Isles, and not, as thought hitherto, only an escape from captivity.

Tucker, B. W. (1949). 'Species and subspecies: a review for general ornithologists.' Brit. Birds, 42: 129–34, 161–74, 193–205.

An important summary of recent advances in the concept of species and subspecies with particular reference to birds.

Waloff, N. (1950). 'The egg pods of British short-horned grasshoppers (Acrididae).' Proc. R. Ent. Soc. Lond. A, 25: 115–26.

Characters used in the classification, key to the egg pods, descriptions and notes on the ecology of the egg pods.

Whatmough, G. W. (1950). 'Notes on collecting and preserving spiders.' Trans. Lincs. Nat. Union, 12: 175–7.

Wilson, G. F. (1951). 'Systemic insecticides.' J. R. Hort. Soc. 76: 165–8.

Systemic insecticides are chemical substances which are absorbed by plants and translocated to all parts of them, rendering these insecticidal. They include selenium compounds, compounds containing fluorine, and organic phosphorous compounds, and are effective for use against aphids and other plant pests.

3. PARASITES

Evans, G. O. (1951). 'The seasonal incidence of *Ixodes ricinus* (L.) on cattle in Mid-Wales.' Bull. Ent. Res. 41: 459–68.

Two peaks, one in the spring, the other in the autumn. No evidence for a unimodal curve of tick activity in this region.

Evans, G. O. (1951). 'The distribution and economic importance of *Ixodes ricinus* (L.) in Wales and the Welsh border counties with special reference to N.W. Cardiganshire.' Bull. Ent. Res. 41: 469–85.

Ixodes ricinus is the common tick, *Dermacentor reticulatus* being recorded on two farms in north Cardiganshire. Marginal and hill farms are most extensively infested. In lowland areas infested pastures are confined to isolated tracts of badly managed or poorly drained land. Degree of infestation of cattle depends on the relative area of the available grazing land colonized by the tick.

O'Rourke, F. J. (1950). 'The isopod *Platyarthrus hoffmanseggi*, Brandt, and its relation to ants.' Ent. Rec. 62: 28–30.

P. hoffmanseggi was attracted towards the highest concentration when placed in a gradient of formic acid (0–10%), but not when in one of propionic acid. *Oniscus asellus* did not move towards formic acid. Since 16 of the ants with which *Platyarthrus hoffmanseggi* is associated in Europe secrete formic acid but nine do not, this acid cannot be the only means by which it is attracted to the nests. Two individuals taken from a nest of *Myrmica laevinodis* lived for 3 months in one of *Leptothorax acervorum*.

4. FOOD AND FOOD HABITS

Ardley, M. J. (1949). 'House-martins feeding at night.' Brit. Birds, 42: 88.

Delichon urbica feeding on small moths at 2 a.m. G.M.T. in July.

Attlee, H. G. (1949). 'House-sparrows feeding on dragonflies.' Brit. Birds, 42: 85.

Passer domesticus taking immature *Brachytron pratense* and *Ischnura elegans*. Attempts to capture mature large species such as *Libellula depressa* usually fail.

Barnes, H. F. (1950). 'Worm eating slugs in Bedford gardens.' Bedfordshire Nat., 4: 24–6.

Testacella haliotidea and *T. scutulum* and their methods of eating earthworms.

Barnes, J. A. G. (1949). 'Feeding behaviour of black-headed gulls.' Brit. Birds, 42: 334–5.

Feeding behaviour in *Larus ridibundus* and *L. canus* similar to that described by Hussey (1949, Brit. Birds, 42: 28). An editorial note suggests that the behaviour is commoner than the paucity of published records suggests.

Betts, A. H. (1949). 'Common gull "hawking" insects.' Brit. Birds, 42: 335.

Larus canus and *L. ridibundus* 'hawking' for flying insects. *L. fuscus* passed through the swarms taking insects, but did not 'hawk'.

Bird, C. R. & Harper, C. G. (1949). 'Common gull diving for food.' Brit. Birds, 42: 222.

Larus canus diving for vegetable food in fresh water.

Brown, D. H. (1949). 'Glaucous gull diving for food.' Brit. Birds, 42: 95.

Larus hyperboreus diving in about 3 ft. of water at Eastbourne.

Brownlow, H. G. (1949). 'The under-water movements of the dipper.' Brit. Birds, 42: 69–73.

A discussion of mechanical aspects of the under-water feeding habits of *Cinclus cinclus*.

Butler, E. M. & Fincher, F. (1949). 'Blackbirds, song-thrushes and starlings taking hairy caterpillars.' Brit. Birds, 42: 88.

Blackbirds (*Turdus merula*), song-thrushes (*T. ericetorum*) and starlings (*Sturnus vulgaris*) feeding regularly on the larvae of garden tiger moth (*Arctia caja*).

Campbell, H. F. (1949). 'Hoopoe in Co. Cork killed by sparrow-hawk.' Brit. Birds, 42: 24–5.

Accipiter nisus taking *Upupa epops* after four attempts.

Chappell, B. M. A. (1949). 'Pied wagtail feeding young on fish.' Brit. Birds, 42: 87.

Cornish, A. V. (1949). 'Nuthatches "hawking" insects.' Brit. Birds, 42: 56.

Two *Sitta europaea* catching insects on the wing.

Dickens, R. F. (1949). 'Moorhen as prey of tawny owl.' Brit. Birds, 42: 153.

Goodwin, D. (1949). 'Jays eating plane buds.' Brit. Birds, 42: 242–3.

Garrulus glandarius and *Passer domesticus* eating the buds of *Platanus* and other trees.

Fife, G. F. (1949). 'Starlings feeding on caddis larvae.' Brit. Birds, 42: 327.

Fisher, J. & Hinde, R. A. (1949). 'The opening of milk bottles by birds.' Brit. Birds, 42: 347–57.

The first record of this habit is from Hampshire in 1921, and it has since spread over practically the whole of Great Britain south of the Great Glen and to the Belfast and Dublin districts of Ireland. The records collected, mainly through the British Trust for Ornithology, support the view that the practice was begun by comparatively few individual birds, and that the vast majority learned it in some way from others. The habit is found principally among the tits, mainly *Parus caeruleus* and *P. major*, but there are records of seven other species both opening and drinking from milk bottles.

Gough, H. C. & Dunnett, F. W. (1950). 'Rabbit damage to winter corn.' Agriculture, 57: 374–8.

Characterization of damage. Effect of rabbit grazing.

Huxley, J. S. (1949). 'Wren feeding young on fish.' Brit. Birds, 42: 185–6.

Troglodytes troglodytes taking fry of *Salmo trutta* at a hatchery.

Ingram, C. (1949). 'Great skua's method of killing large birds.' Brit. Birds, 42: 223.

Stercorarius skua attacking and partially eating an adult *Tadorna tadorna*, and killing other large birds.

Kennedy, J. S. & Booth, C. O. (1951). Host alternation in *Aphis fabae* Scop. I. Feeding preferences and fecundity in relation to the age and kind of leaves.' Ann. Appl. Biol. 38: 25–64.

Experimental, but includes important discussion of the dual discrimination theory of host selection—one discrimination between properties associated with the age of a leaf, the other between properties associated with kind of leaf.

Knight, M. (1948). 'The study of bird pellets as a subject of interest and instruction to amateur naturalists.' S. East. Nat. 53: 53–60.

Information on the function of pellet-formation and photographs of pellets of carrion-crow, rook, raven, gull, kestrel, buzzard, heron and three owls.

Laurence, B. R. (1949). 'Bees and delphiniums.' Bedfordshire Nat., 3: 43–4.

Feeding methods of *Bombus* spp. visiting garden delphiniums. Of 464 flowers examined at random, 55% had their spurs pierced by Hymenoptera.

Laurence, B. R. (1950). 'Predators and prey.' Bedfordshire Nat. 4: 27–30.

Records of prey of Asilidae, Empididae, Cordiluridae and *Coenocia* (Muscidae).

Oliver, J. C. C. (1950). 'Spotted flycatcher pellets.' Bedfordshire Nat. 4: 52.

Description and contents of 20 pellets.

Richards, T. J. (1949). 'Concealment of food by nuthatch, coal-tit and marsh-tit.' Brit. Birds, 42: 360–1.

Sitta europaea, *Parus ater* and *P. palustris* hiding or burying beech-mast.

Roebuck, A. (1950). 'Notes on the economic zoology of Lincolnshire during 1949.' Trans. Lincs. Nat. Union, 12: 164–7.

Notes on the food of various insect pests, with a few other animals.

Ryves, B. H. (1949). 'Greenfinch taking seeds from pine cones.' Brit. Birds, 42: 212.

Chloris chloris and *Fringilla coelebs* feeding on the seeds of *Pinus insignis*.

Williams, E. M. (1949). 'Nuthatch "hawking" insects.' Brit. Birds, 42: 386.

With an editorial note suggesting that the habit is not so unusual as the lack of published records suggests.

5. POPULATION STUDIES

Alexander, W. B. (1949). 'The index of heron population, 1948.' Brit. Birds, 42: 81–3.

This annual report, based on a sample census of the population of *Ardea cinerea* in the British Isles, shows an increase of 2% over 1947. There is a range of variation from an 11% increase in the Midlands to a 9% decrease in south-east England.

Campbell, B. (1951). 'A colony of stock-doves.' Bird Notes, 24: 169–76.

A population study of *Columba oenas* in an Oxfordshire barn during 1949–50.

Ibbotson, A. & Kennedy, J. S. (1951). 'Aggregation in *Aphis fabae* Scop. I. Aggregation on plants.' Ann. Appl. Biol. 38: 65–78.

The clustered distribution of aphids on the leaves of its host plant involves active aggregation and is not chance. The unequal distribution among the leaves of a plant is due primarily to intrinsic differences between leaves and is aided by gregariousness. That on the leaves is due primarily to gregariousness and only secondarily to differences between portions of the leaves.

Lack, D. (1949). 'The apparent survival-rate of ringed herons.' Brit. Birds, 42: 74–9.

An average of 1·7 young die in each heron's nest between late April and early May, and the time of leaving the nest at the end of June, when survivors average 2·1. By this time there is an expectation of further life of 1·5, and at the beginning of the second year of life the expectation of survival is for 2·8 years. Factors tending to bias the results are discussed.

Lack, D. (1949). 'Vital statistics from ringed swallows.' Brit. Birds, 42: 147–50.

A study based on the ringing schedules of the British Trust for Ornithology. The average annual mortality of the swallow is shown to be 63%, and its expectation of life on the first 1 January of life, 1·1 years. The average size of broods decreases from 4·06 in June to 3·50 in September.

Lack, D. & Silva, E. T. (1949). 'The weight of nestling robins.' Ibis, 91: 64–78.

Nestlings of *Erithacus rubecula* were weighed daily. Size of brood appeared to have no influence on the weight of individual nestlings. Large broods appeared to be fed by the parents rather more often than small broods, but the feeding-rate did not increase proportionately to the greater number of young. See also Lees (1949, Ibis, 91: 79–88, 287–99).

Lees, J. (1949). 'Weights of robins. Part 1. Nestlings. [Part 2. Juveniles and adults.]' Ibis, 91: 79–88, 287–99.

Weights of *Erithacus rubecula* in the nestling, juvenile and adult stages, with observations on changes in the local population. See also Lack & Silva (1949, Ibis, 91: 64–78).

May, D. J. (1949). 'Studies on a community of willow-warblers.' Ibis, 91: 24–54.

A study of a community of *Phylloscopus trochilus* on a Surrey common over 3 years, with a population study in 1 year. Territory seems to limit the population. The female appears to select the nest site. In each year, 55–58% of the eggs laid produced young birds that left the nest.

Silva, E. T. (1949). 'Nest records of the song-thrush.' Brit. Birds, 42: 97–111.

A statistical study of *Turdus ericetorum* based on the nest record cards of the British Trust for Ornithology. The average clutch-size in Britain increases from mid-March (3·9) to a peak in May (4·4), and then declines to 3·4 in mid-July when breeding normally ends. The average incubation period is 13·4 days, and nestling period, 13·2 days.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Aitkenhead, P. (1951). 'The Gladiolus thrips—a pest new to Britain.' Agriculture, 57: 517–22.

Life history, host plants and map of distribution of *Taeniothrips simplex*.

Bedford, Duke of (1950). 'Deer in Britain.' Bedfordshire Nat. 4: 12–20.

A general account, with references to several recently introduced species, including sika, muntjac and water-deer.

Boswall, J. H., Brown, D. H. & Harber, D. D. (1949). 'The spring movement of brent geese in Sussex.' Brit. Birds, 42: 90–1.

An eastward passage at sea of *Branta bernicla* was noted from the shore on eight days between 26 March and 30 April, also on 16 May and 16 June 1948.

Brady, F. (1949). 'The fluctuations of some common shore-birds on the north Northumberland coast.' Brit. Birds, 42: 297–307.

Counts of waders over 3 years, revealing several waves, evidently due to migrating birds.

Brown, P. E. (1949). 'The breeding of avocets in England, 1948.' Brit. Birds, 42: 2–12.

Recurvirostra avosetta bred successfully in East Anglia for the second year in succession. At least nine pairs nested at two sites, and thirteen young were reared. Details of behaviour at the nesting site are also given.

Cooper, J. R. (1949). 'Siskins breeding in Westmorland.' Brit. Birds, 42: 22.

Certainly three, and possibly five or six pairs of *Carduelis spinus* bred in 1946 in the Ullswater district, representing a southward extension of range.

Cox, S. A. (1949). 'Bittern breeding in Lincolnshire.' Brit. Birds, 42: 392–3.

An extension of range; 'booming' was first noticed in 1941–2, but breeding not proved till 1949.

Edmondston, T. (1951). 'Studies of the inland spring migration of selected Passerines in South Lancashire.' Naturalist: 41–4.

An analysis of the records obtained by observing the spring passage of the yellow wagtail, white wagtail, wheatear, swallow and sand-martin at Leigh Flash. These show that there is a marked migration from mid-April to mid-May and that well-defined waves occur.

Fitter, R. S. R. (1949). 'Report of the Black Redstart Inquiry for 1948.' Brit. Birds, 42: 206–7.

More pairs of *Phoenicurus ochrurus* bred in south and east England than in any previous year (26–29). There is a tendency for small breeding populations to become established in a few localities, and for birds to be reported away from the known breeding sites in July and August, before the Continental immigrants arrive.

Fletcher, T. B. (1950). '*Antigastra catalaunalis* in Gloucestershire.' Ent. Rec. 62: 88–9.

A fresh specimen of this rare immigrant Pyraustid moth that may have bred locally was captured near Gloucester in August 1950. There are several plants in this country on which it might feed.

Gimingham, C. T. & Thomas, I. (1950). 'Colorado beetle in England, 1949.' Agriculture, 57: 134–7.

Fewer single finds of *Leptinotarsa decemlineata* than in 1948 and no breeding colonies as compared with 11 in 1948 and 57 in 1947.

Gregory, T. C. (1949). 'Bittern nesting in Kent.' Brit. Birds, 42: 187.

Botaurus stellaris has been attempting to colonize east Kent since about 1938 and breeding was finally proved in 1948.

H[arber], D. D. [1951]. 'Hirundine and swift migration at Langney Point in 1950.' Sussex Bird Rep. for 1950: 27–8.

Hinde, R. A. (1949). 'Exceptional inland passage of black terns in 1948.' Brit. Birds, 42: 113–17.

Records of over 150 flocks containing over 2000 *Chlidonias niger* between 20 April and 5 June, with a peak between 16 May and 22 May. The exceptional numbers were probably due to unusually strong north-easterly winds carrying birds migrating northwards to the west of their track.

Hinde, R. A. & Harrison, J. G. (1949). 'Inland migration of waders and terns.' Brit. Birds, 42: 308–19.

Results of a co-operative inquiry organized by the British Trust for Ornithology in 1947 and 1948. Evidence of waves of migration in each species was obtained, and it was shown that the date of the peak of this wave varies with the breeding season of the individual species.

Höhn, E. O. (1949). 'Tern migration in south Staffordshire in autumn.' Brit. Birds, 42: 254–5.

A movement at a mere and a reservoir 7 miles apart involving two or three species of tern.

Lack, D. & Lack, E. (1949). 'Passerine migration through England.' Brit. Birds, 42: 320–26.

Demonstrates the existence of a concentrated stream of diurnal passerine migrants flying west and south-west along the escarpments of the Chilterns and Berkshire Downs.

Leach, E. P. (1949). 'Recovery of marked birds.' Brit. Birds, 42: 264–76.

A continuation of a series of periodic reports on recoveries of birds ringed in the British Isles.

Orton, J. H. (1950). 'The recent extension in the distribution of the American slipper limpet, *Crepidula fornicata*, into Lyme Bay in the English Channel.' Proc. Malac. Soc. Lond. 28: 168–84.

Crepidula is estimated to have invaded Lyme Bay in 1942 or 1943 (from the East). The possibility of self-fertilization is discussed, and the possible effect on the extension of range.

Romer, M. L. R. (1949). 'Autumn immigration of great tit, blue tit and coal-tit at Dungeness, Kent.' Brit. Birds, 42: 386–7.

Notes indicating that considerable numbers of tits of Continental origin arrive in this area during the autumn.

Whiteley, E. F. (1949). 'Probable breeding of pied flycatcher in Cheshire.' Brit. Birds, 42: 57–8.

A pair of *Muscicapa hypoleuca* seen in June, one of them feeding a fully-fledged young, well away from other known breeding stations of this increasing species.

7. REPORTS OF ORGANIZATIONS

Lundy Field Society (1951). 'Fourth Annual Report, 1950.' 54 pp.

The Society's field work during the year has included work on counts of nesting sea-birds, the local distribution of the snail *Limnaea truncatula* and the longhorn grasshopper *Leptophyes punctatissima*, a survey of small mammals and a preliminary investigation of the Diptera.

Rugby School Natural History Society (1951). 84th Report, for the year 1950. 56 pp.

The census of water birds at Stanford Reservoir was continued, and there are faunistic notes on mammals, birds, reptiles, Amphibia, butterflies and the wood wasp (*Sirex gigas*), evidently introduced with pinewood planks for new shelves.

Severn Wildfowl Trust (1951). Third Annual Report, for 1949–50. 132 pp.

Includes counts of the winter population of wild geese on the Severn estuary, an account of marking operations on geese away from the New Grounds, and general faunistic notes on birds.

Skokholm Bird Observatory (1951). Report for 1950. 28 pp.

Work at the observatory included continuation of the studies of the life history of the wheatear and the oystercatcher. The report includes faunistic notes on the mammals, birds, reptiles, Amphibia, butterflies and Diptera of both Skokholm and Grassholm, and an account of homing experiments with lesser black-backed gulls.

Thomson, A. L. (1949). 'Report of the Bird-Ringing Committee: progress for 1948.' Brit. Birds, 42: 175–80.

The number of birds ringed during the year under the Bird-Ringing Scheme of the British Trust for Ornithology increased from 28,581 in 1947 to 39,324. Numbers of each species ringed, and percentage of recoveries since the start of the scheme are also given.

Yorkshire Naturalists' Union (Vertebrate Section) Committee for Ornithology (1951). 'Report for 1950.' Naturalist, 51–74.

The mild spring meant early breeding of some resident birds and many broods were lost in the bitterly cold April-May. 1714 birds were ringed at Spurn, while ringing was also carried out at the High Royd and Ben Rhydding ringing traps and in the forests of north-east Yorkshire.